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ONE HUNDRED YEARS OF THE MISSOURI BOTANICAL GARDEN[1,2]

Emanuel D. Rudolph[3]

ABSTRACT

In the hundred years since the Board of Trustees of the Missouri Botanical Garden implemented the stipulations of Henry Shaw's will, which prescribed functions for his public garden and provided an appropriate endowment, six directors have guided the Garden's development. Henry Shaw's (1800–1889) vision of the Garden was based upon his British background and the European botanical garden tradition. William Trelease, the first director (from 1889 to 1912), set his highest priorities on building the herbarium and library and publishing substantial annual volumes, which he believed would make the Garden a major center for taxonomic research. George T. Moore, director for 40 years (from 1912 to 1953), moved the research into other areas of botany, applied botany, and horticulture. Keen on public display yet facing decreasing finances toward the latter part of his tenure, he began to seek private support for various programs, including a new arboretum located outside the city. The short duration of Edgar Anderson's directorship (1954–1957) was focused on Garden improvements with further attempts to raise funds and find support among garden clubs. Frits Went, the fourth director (1958–1963), saw the Garden as a potential multifaceted cultural center for St. Louis. The geodesic domed greenhouse, named the Climatron, opened in 1960 as a major implement in concentrating local and national attention on the Garden. The fifth director, David Gates (1965–1971), moved the Garden into ecological research and found support for a new research building that had been sought by Went. The current director, Peter H. Raven (1971 to the present), has moved the Garden along on various fronts. He has expanded its horticultural displays and special gardens, widened the base of public support, enhanced the research in systematic botany, and projected the role of the Garden into international efforts to understand our biosphere and protect it. Each director has guided the Missouri Botanical Garden in certain directions during the last hundred years to make it the major botanical garden that it now is.

Thinking sentimentally back to his youth at the Mill Hill School in England, Henry Shaw, then in his seventies, sat in Tower Grove House looking out over his St. Louis Public Botanical Garden and wrote:

"Peter Collinson . . . had a house and garden at Mill Hill . . . ten miles from London, and was one of the chief encouragers of gardening and planting in his time . . . . Collinson died in 1768 at the age of 74 years, and some time after his death the house and grounds were purchased by the Protestant Dissenters Associa-

[1] This and the five articles that follow it are the proceedings of the 36th Annual Systematics Symposium of the Missouri Botanical Garden, *A Century of Botany: 1889–1989*. The symposium was held 6–7 October 1989 at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

[2] The staff of the library and archives of the Missouri Botanical Garden are gratefully acknowledged for unfailing assistance and hospitality. The use of the archives and special collections of the Royal Botanic Gardens, Kew, the Gray-Arnold Arboretum and Farlow libraries of Harvard University, and Cornell University Library are gratefully acknowledged.

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tion for a school for classics and mathematics . . . . Collinson's large Green-house had been altered into a classroom, at one end of which the window still remained, looking from his library into the Green-house below. In 1812 many fine specimens of rare plants still grew in the garden, with the Cypress of Linnaeus; but the most admired trees were the noble Cedars of Lebanon that grew near the play ground, protected from injury by a high board fence. Nearby were the boys' little gardens of about 25 feet square each, well fenced to guard against the intrusions of the football; for those that preferred gardening for a recreation, of which number was—The writer of this Guide—who from 1812 to 1815 thus releived fugging [sic] at Latin Greek and Euclid, by growing pinks and geraniums, and retiring to a seat in a corner of his little domain, shaded by a broad trained Irish yew, purchased from a neighboring nursery at the price of ten shillings. . . . The writers studies at Mill Hill, endeared by many pleasing recollections, ended the day that the Great Napoleon's ambitious career closed, by the memorable battle of Waterloo, in June 1815, and returning home to Sheffield in the Great Northern Mail coach, drawn by four spanking grays, bedecked with greens and ribbons that carried the glorious news of victory to the joyful people of Scotland and North Britain."[4]

The wealthy bachelor Shaw (Fig. 1) had worked for more than 40 years before his death in 1889 to perfect his gift of a garden for the people of St. Louis, Missouri, and the nation.[5] Perhaps he thought about Peter Collinson's garden, which he knew was mostly lost to posterity. After retirement from his active hardware and dry goods business in 1839, Shaw invested his funds in sound St. Louis real estate and other business ventures, which increased his wealth.[6] Between 1840 and 1852 he made three extensive European trips, which included visiting gardens in different countries. In time, he settled upon making a botanical garden, rather than a pleasure garden, on part of his country land in St. Louis.

Botanical gardens have a long and noble tradition dating from Renaissance times.[7] Their early particular function was to cultivate plants with medicinal uses and those that served as living texts for learning about materia medica. Thus, they were mostly connected with university medical schools or apothecary guilds. The earliest botanical gardens at Padua and Leyden were laid out in the form of four large beds making a cross pattern with their major paths. The cross is significant not only for its religious connotations, but also because it divided the garden into the four great world divisions then known: Europe, Asia, Africa, and the Americas. Here then was the world encompassed; God's munificence to humans from all corners of the globe displayed (Fig. 2).

In time, it became evident that not all plants did well under the same conditions. Later botanical gardens, such as the Jardin Du Roi in Paris, had varying habitats, some wet, dry, sunny, and shaded. In fact, it was what we call today an ecological approach to plant cultivation which by this time included all sorts of plants, not only medicinal ones (Fig. 3). By the eighteenth century, learning about God's creation was a worthy endeavor in itself, one that could only magnify the deity.[8]

When Henry Shaw traveled in Europe, there were numerous botanical gardens that served as models. Not surprisingly, his British background led him in 1854 to contact Sir William Jackson Hooker, the director of the Royal Botanic Gardens, Kew.[9] In time, Shaw emulated some aspects of Kew, for example, by building a museum building, and plant houses, and later an orangery—the Linnean House—based upon Kew models. However, as he wrote to Hooker, he did not have in mind the extensive size and broad activities of Kew, but rather a garden of more modest dimensions such as those of Glasgow or Liverpool.[10] Hooker put Shaw in contact with Asa Gray at Cambridge and George Engelmann at St. Louis. They gave him advice and encouragement.[11]

On a European trip in 1857 Engelmann purchased the herbarium of some 40,000 specimens from the estate of the recently deceased Johann Jacob Bernhardi, and found botanical books for Shaw.[12] These botanical resources, later including the herbarium and library of Engelmann after his death, were dutifully kept, but little used, in the Museum Building (Fig. 4), which then displayed stuffed animals and oil portraits of important botanists.[13] These portraits can now be seen on the Garden's library walls.

Shaw concentrated his efforts on the horticultural aspects of the garden. With the aid of his Kew-trained gardener James Gurney, he planted outdoor beds of ornamentals, a fructicetum of shrubs and fruit trees, and an arboretum of trees. The plan was to divide the garden into the three great groups of plants; herbs, shrubs, and trees. In addition, plants needing protection were housed under glass (Fig. 5). By the time of this death in 1889, Henry Shaw had established a considerable public

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FIGURE 1. Henry Shaw at about age 87, from an oil painting at the Missouri Botanical Garden, painted by Fairchild and Fox.

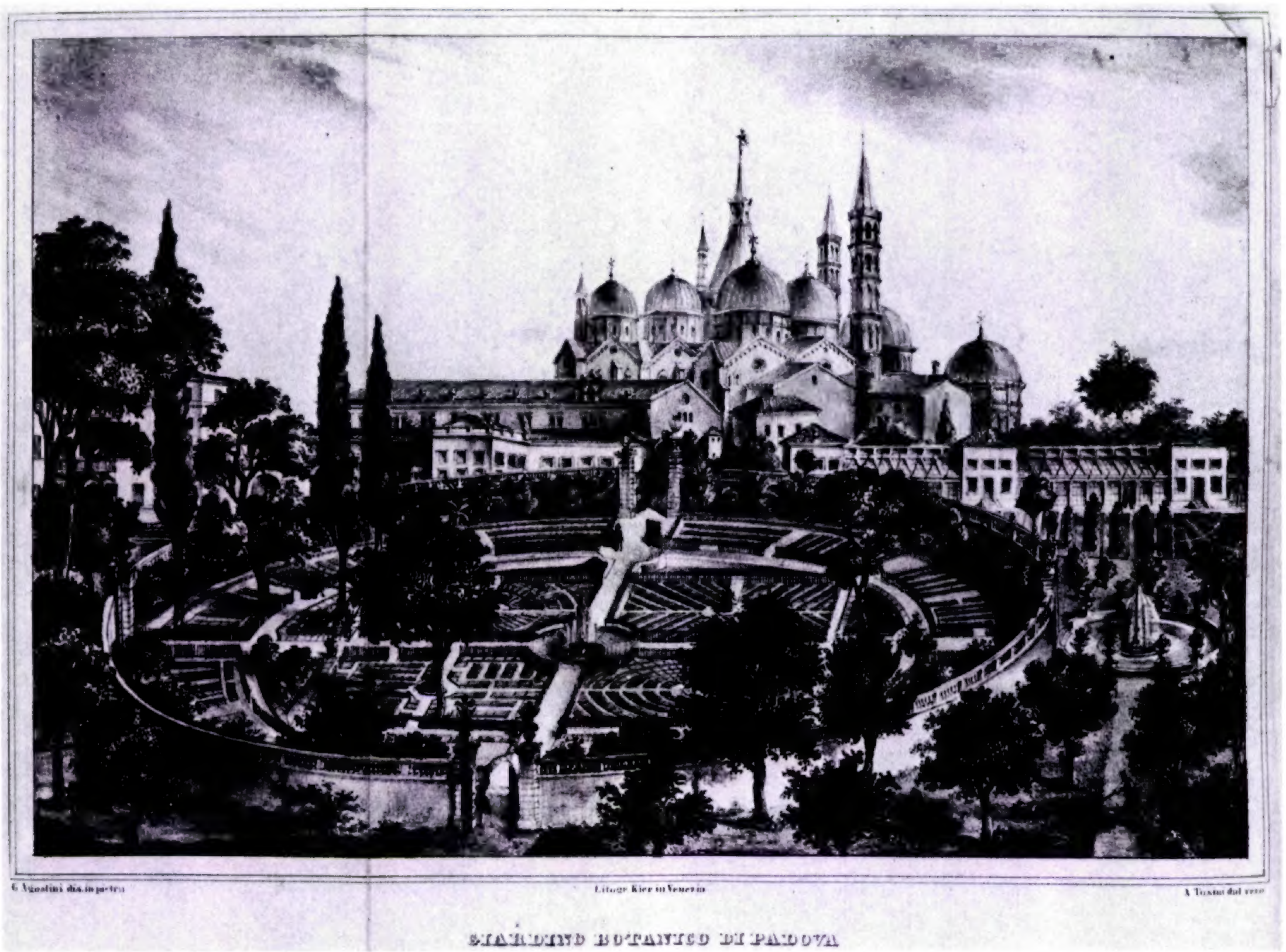

FIGURE 2. Plan of the botanical garden at Padua, from R. de Visiani, *L'Orto botanico dei Padova nell'anno MDCCCXLII*, Padua, Angelo Sicca, 1842. (Courtesy of Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh, Pennsylvania.)

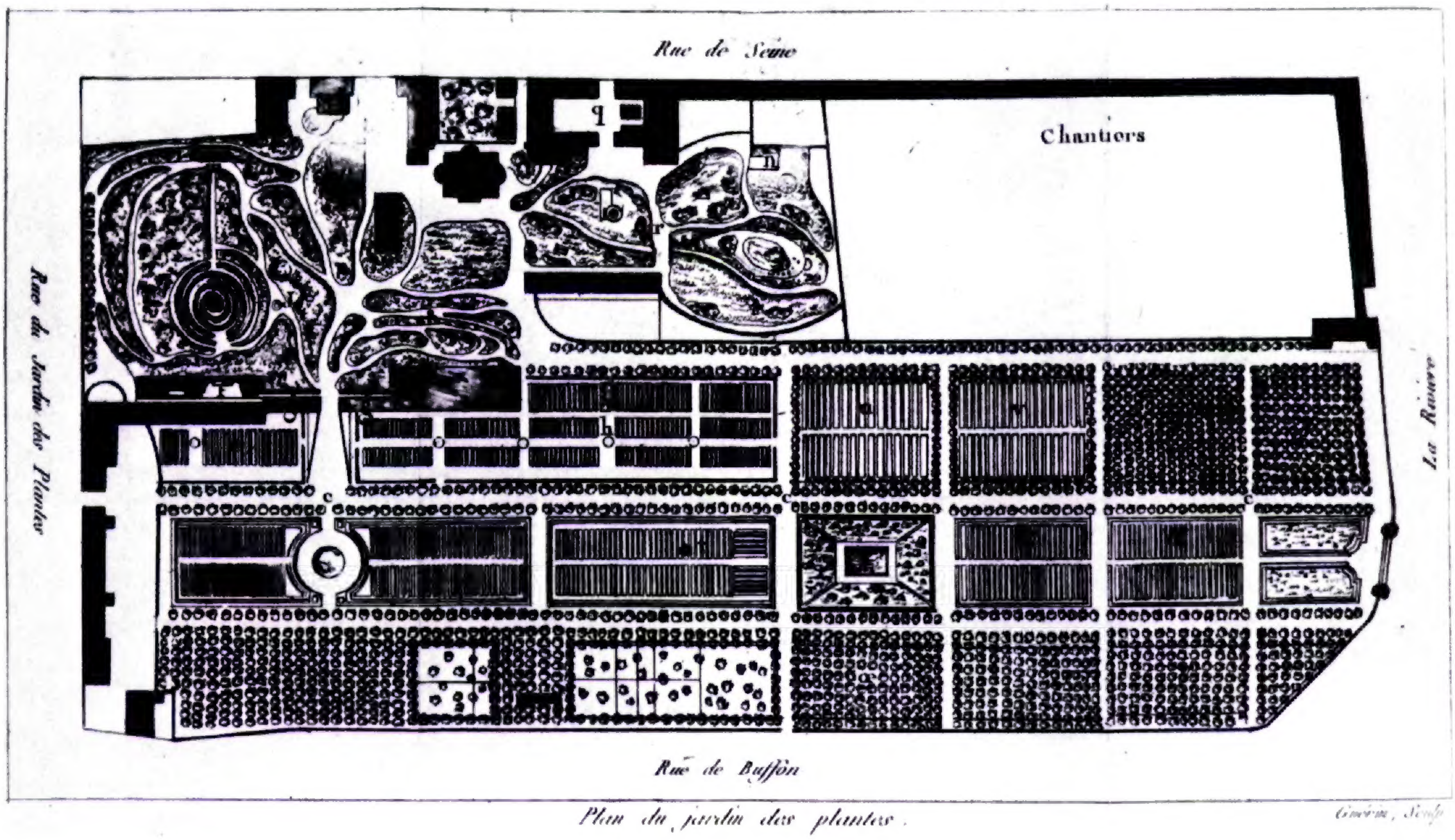

FIGURE 3. Plan of Jardin des Plantes when the Jardin du Roi, from J. B. Pujouix, *Promenades au Jardin des Plantes, à la Ménagerie et dans les Galeries du Muséum d'Histoire Naturelle* . . . Troisième édition, Paris, Librairie Economique, 1803. (Tome premier.) (Courtesy of Hunt Institute for Botanical Documentation, Carnegie Mellon University, Pittsburgh, Pennsylvania.)

THE MUSEUM—SHAW'S GARDEN.

FIGURE 4. The Museum Building at the Missouri Botanical Garden during the lifetime of Henry Shaw, from J. A. Dacus & James W. Buell, *A Tour of St. Louis; or, the Inside Life of a Great City*, Western Publishing Co., St. Louis, 1878.

botanical garden adjacent to his country villa, Tower Grove.[14] Property nearby had been given to the city to develop, with his advice and assistance, an elaborate pleasure park with walks and roads, Tower Grove Park.[15]

With significant input from Asa Gray, who visited Henry Shaw in 1884 and again in 1885, aiding him in his plans, Shaw drafted a will in 1885.[16] It provided that upon his death the Missouri Botanical Garden, founded by him and approved by the General Assembly of The State of Missouri in 1859,[17] would have income from an endowment to be administered by a self-perpetuating Board of Trustees, which appoints the director to oversee the running of the Garden. It states that the Garden, "should be forever kept up and maintained for the cultivation and propagation of plants, flowers, fruit and forest trees, and other productions of the vegetable kingdom; and a museum and library connected therewith, and devoted to the same and to the science of botany, horticulture, and allied objects . . . ."[18] At Gray's suggestion, Shaw decided a set yearly stipend for support of a botany school at Washington University, to be known as The Henry Shaw School of Botany, and a professorship, to be known as the Engelmann Professor.[19]

William Trelease, then a professor of botany at the University of Wisconsin, was appointed the first Engelmann Professor and Director of the School in 1885. When the Trustees met upon Shaw's death in 1889 to carry out the terms of his will, Trelease was also immediately selected to be the first director of the Missouri Botanical Garden (Fig. 6).[20] A northeasterner with an undergraduate degree in entomology from Cornell University under John Henry Comstock (1880) and a doctorate from Harvard University under William Gilson Farlow (1884), Trelease was recommended by Gray and others as the most suitable person to lead the new school of botany. Trelease had already made a name for himself in published studies of insects, pollination, fungi, and plant morphology. His doctoral thesis on bacteria was the first on this group in America, and his bacteriology course at Wisconsin was perhaps the first one offered there. He had strong connections with the Eastern Coast bo-

INTERIOR OF PLANT HOUSE.

FIGURE 5. Inside view of the Plant House during Henry Shaw's lifetime, from J. A. Dacus & James W. Buell, *A Tour of St. Louis; or, the Inside Life of a Great City*, Western Publishing Co., St. Louis, 1878.

tanical establishment, and through his Wisconsin experience, some midwestern ties.

Trelease proved to the ideal person to implement the spirit and substance of the Shaw–Engelmann–Gray vision of the Missouri Botanical Garden. Once moved into the Tower Grove House, Trelease quickly realized the serious problems with the Garden's physical plant. He at once began to improve the grounds and buildings with the help of James Gurney. Trelease also initiated a strong research and teaching program. He built a substantial herbarium of plants from the southwestern states by collection and purchase, and made monographic studies, as did others at the Garden, on plants of the region.

Imagine the Garden in the year of the Louisiana Purchase International Exposition in 1904. This largest and most elaborate World's Fair up till that time[21] drew many to St. Louis and to the Garden. Trelease, after his 14 years as the director, was proud of the Missouri Botanical Garden. Once inside the gate in the high stone wall around the Garden visitors would find that "11,357 species and varieties of plants were in cultivation."[22] After

visiting the outside garden, lily pools, some with the large *Victorias*, a large area with native American flowers, an orchard, a fructicetum, and a large arboretum, one could enter a number of recent interconnected greenhouses. Some outside plantings and greenhouses were devoted to yuccas and agaves, which both Engelmann and Trelease studied. Tower Grove House, with a wing added in 1890, was the director's residence. Shaw's city house, rebuilt at the Garden in 1891, contained the offices, and much of the herbarium and library; an added wing was to be built in 1909. Some of the herbarium and library still were housed in the Museum Building, which also included a few laboratories.

Trelease had put most of his energy into building a sound foundation for the future research and teaching programs. The herbarium in 1889 consisted of about 160,000 specimens, many unprocessed, from the Bernhardi, Engelmann, and Nicholas Riehl collections; in 1904 it had five times the number, or about 490,000 specimens.[23] Included were purchases or gifts of some major collections made by Ferdinand Blanchard, Farland Carr Broadhead, Samuel Botsford Buckley, Benjamin Franklin Bush, Alvan Wentworth Chapman, J. Q. Adams Fritchey, Gustav Jermy, Joseph Finley Joor, Sadie F. Price, John Howard Redfield, the Reverend Ernest C. Smith, E. Lewis Sturtevant, George Thurber, as well as Trelease's own collections. The library in 1889 had about 428 volumes from Henry Shaw's purchases and other books, some from George Engelmann's library, totaling about 3,000 volumes; in 1904 it had 45,815 volumes or an increase of over 15 times.[24] But numbers alone do not tell the whole story. In 1892 E. Lewis Sturtevant donated an important collection of 463 pre-Linnaean books and his own manuscripts and notes. Then in 1902, a large collection of pre-Linnaean books was purchased from a German bookseller. Together, these collections made the Garden a significant repository of early botanical literature. Jens Christian Bay, newly arrived from Denmark, was hired to prepare a catalog of the Sturtevant Collection.[25] Bay was later to become the librarian at the Crerar Library in Chicago. The catalog was published in the *Missouri Botanical Garden Annual Report*, a publication that served from 1890 until 1912 as an outlet for publishing Garden research results. Scientific research was the primary goal of Trelease's plans, and he himself had begun major monographs of *Yucca* and *Agave* done when he had time to travel and do research.

Specialization in herbarium collections had begun. Because the Engelmann herbarium was strong

FIGURE 6. William Trelease in 1903 at age 46. (From the archives of the Missouri Botanical Garden.)

in plants of Texas and the Southwest, these collections were selectively increased by collecting expeditions. It is interesting to note that a start was made on an African collection by paying S. P. Verner, who had brought African Pygmies to the World's Fair, to collect plants in the Upper Congo.[26]

Bright young students were employed as assistants by Trelease. Some of them were to become important botanists: Albert Spear Hitchcock, Lewis Hermann Pammel, Frederick Hinsdale Horsford, and J. Arthur Harris. He encouraged Hermann von Schrenk, a plant pathologist associated with the United States Department of Agriculture, to locate his laboratory at the Garden, where he maintained it for 50 years.[27]

Though it was difficult to get a new major graduate teaching program instituted, a school for gardeners was quickly established. This was one of Shaw's designated programs, probably because he and Asa Gray had so much trouble finding well-trained American gardeners.[28] This significant school was to last into the 1930s.

The successful 1904 World's Fair led to op-

FIGURE 7. The Missouri Botanical Garden/Mill Hill School exhibit at the Louisiana Purchase International Exposition, St. Louis, 1904. (From the archives of the Missouri Botanical Garden.)

portunities for the Garden.[29] The Garden had an exhibition in association with the Mill Hill School, which showed living plants, preserved local mushrooms, pictures of the Garden and Shaw, and Garden publications (Fig. 7). This exhibit, together with various living flowers that won awards in competitions, gave the Garden favorable publicity. At the close of the Fair, some of the exhibitors provided exotic living plants, thus increasing the Garden's holdings from such countries as Brazil, China, Cuba, and the Philippines.[30]

Trelease was successful in establishing a superb reputation for the Garden in the botanical scientific community. He was less successful in convincing the Board of Trustees that his was the right direction. In 1912, as a result of increasing disagreement with the Board, Trelease resigned. The disagreements had become acute a year before when a new president of the Board was elected and, as Trelease wrote to his mentor Farlow, he was advised that "we're going to have more garden and less science, now."[31] Trelease was not willing to compromise his principles, and his resignation by agreement was announced as a "retirement" to do research, few knowing the real reasons. George T. Moore, who had been brought in by Trelease in 1909 as professor of plant physiology in the plans to expand the graduate program, became the new director. Trelease also had hired George Pring, a Kew-trained gardener who was later to make a reputation as a water lily breeder, to be in charge of orchids and exotics.[32] Some able people were still in charge, but programs were in need of further implementation.

George Thomas Moore (1871–1956; see Fig. 8) was a midwesterner by birth and early education, with an undergraduate degree from Wabash College in Indiana in 1894.[33] His graduate training was from Harvard University, working with William G. Farlow (A.M. 1896, Ph.D. 1900), and then teaching at Dartmouth College in New Hampshire (1899–1901). He was algologist and plant physiologist with the Bureau of Plant Industry, United States Department of Agriculture, from 1901 to 1909, and was in charge of its plant physiology laboratory since 1902. Moore's background made him an ideal selection for Trelease to put in charge of the graduate program at the Garden and Washington University in 1909. Moore's research was with algae and bacteria, both

FIGURE 8. George Thomas Moore after becoming director of the Missouri Botanical Garden. Photographed by S. D. Whiting. (From the archives of the Missouri Botanical Garden.)

pure and applied. At the Bureau of Plant Industry he perfected methods to rid water supplies of pesty algae, and to inoculate plants with nitrogen-fixing bacteria. He was a skillful speaker, writer, teacher, and promoter of botany.

It was no wonder that Moore impressed the director's search committee of the Board with his clear descriptions of what needed to be done at the Garden.[34] He had the ability of being able to speak to businessmen on their own terms. For example, after being the director for three years, he told the Board that ". . . the increase in the service of the activities, such as the herbarium, laboratories, etc., has been quite as great as the increased number of visitors. As a matter of fact, the development of what may be termed the strictly scientific side of the Garden shows more tangible results for the amount of money which is annually devoted to this purpose than the Garden proper; and so far as a return upon the investment is concerned, may always be expected to be the most fruitful of the Garden activities."[35] He at once set out to improve the show aspects with frequent floral displays, well-kept grounds, and innumerable press releases producing publicity that attracted large crowds. By using comparisons with other institutions in St. Louis and elsewhere, by stressing practical uses of research, for example cancer research and water and air pollution research, and by persuasion, Moore also was able to expand the scientific and educational programs, something that Trelease had been unable to accomplish. When Jesse M. Greenman was hired by Moore in 1913 to be curator of the herbarium, he was charged with preparing a southwestern flora, a task never completed. Moore soon got on an equal footing with the Trustees by being first an ex-officio member of the Board as the president of the St. Louis Academy of Science in 1918, and then in 1928 by being elected as a lifetime regular Trustee.[36] Further, because the Board had so much confidence in his abilities, he was able to eliminate the required monthly budget requests, to curtail the written monthly reports of the director, and dispense with the oversight of Garden operations by the Garden committee of the Board. In short, Moore was able to run the Garden with less and less direct supervision by the Trustees.

To examine Moore's achievements, imagine how it would have been to visit the Garden in the middle of his 41-year directorship, in the year 1926.[37] Upon entering through the recently enlarged and redesigned gate, one would find lily pools leading to new large greenhouses, one of which was a floral display house with continuous ornamental displays. In the rear of the greenhouses was an elaborate sunken Italian garden with pergola. A new rose

garden, economic garden, and many simplified manicured ornamental flower beds were well cared for. A director's residence had been built south of the Administration Building.

The scientific staff in 1926 included: Benjamin M. Duggar, plant physiologist; Jesse M. Greenman, curator of the herbarium; Edward A. Burt, librarian (in name only) and mycologist; Edgar Anderson, geneticist, also in charge of the Gardeners' School; Hermann von Schrenk, plant pathologist; and a second mycologist, David H. Linder, Farlow's nephew, soon to be replaced by Carroll W. Dodge from Harvard. Scientific programs were active, with results being published in the quarterly *Annals of the Missouri Botanical Garden* initiated in 1914 to replace that function in the old *Annual Reports*. Information and popular articles now appeared in the *Bulletin*, started in 1913. An active research project was collecting and studying the Southwestern flora, concentrated on the plants of Missouri, Arkansas, and Texas. Julian Steyemark, a graduate student, was to study the Missouri flora then, and for years to come.[38] A newly opened tropical station of the Garden in Balboa, Panama Canal Zone, encouraged plant collecting and the flora of Panama project later to develop.[39] Research in plant physiology, particularly of fungi, plant pathology, mycology, and plant breeding was in progress. Moore gave up his active research to spend time in administration, teaching, and public speaking.

The Garden was becoming noted in horticultural circles for its water lily and orchid hybridization. Collected and donated orchids had made the Garden preeminent in this country for its extensive living collection of orchid species.[40] James Gurney and George Pring were active in the hybridizing program. Unfortunately, the excessive smog of soft coal particles was damaging outside plantings and indoor orchids. The orchids were not only important for displays, but also for income by supplying local florists. Moore campaigned with those in the city who sought smoke abatement laws, but progress was slow.[41] As a result of the smoke problem, the Trustees, with the court's approval, sold land adjacent to the Garden in order to purchase an out-of-town site for plants, particularly for trees, and greenhouses for orchids. In 1925, extensive property on the Meramec River at Gray Summit was purchased, to be called at a later date the Shaw Arboretum.[42]

In 1926 the future for the Garden seemed bright. However, in a few years that was to change drastically. The Great Depression affected value and income from the properties from which the Garden's operating funds came. Even after the Depression had abated, these properties did not recover enough to help the Garden recover. Moore was getting older and less energetic. He kept up a good front at the same time that he was economizing by moving the plant physiology to the university, decreasing the number of gardeners, cutting the number of floral displays, and limiting the budget for library, herbarium, and grounds. Edgar Anderson was to write of this period that Moore "... retrenched as skillfully as he advanced,"[43] which meant that many did not realize the seriousness of the Garden's problems. Moore attempted to raise funds through his extensive social contacts, and by the formation in 1939 of a Friends group. However, because of the immense needs for repairs, replacement, and catching-up, these efforts turned out to be insufficient. Then, too, Moore's health deteriorated and Edgar Anderson was made assistant director in 1951. The Trustees seemed to be little involved with solving the problems.

In short, the Missouri Botanical Garden was in the doldrums in 1953 when a new Board president, John S. Lehmann, was elected and when Moore became Director Emeritus. The scientific community scarcely realized the situation because many of the research programs and their publications continued, including the *Flora of Panama*, even though the tropical station had closed some years earlier. But the physical plant and gardens were in disrepair.

The directorship of Edgar Anderson (Fig. 9), which began in 1954, was to last only a few years; however, Anderson and his assistant Hugh Cutler made significant changes. Anderson's long connection with the Garden began in 1922 when he came as geneticist and assistant professor at Washington University, fresh from the Bussey Institution of Harvard University with a doctor of science degree.[44] He was also in charge of the gardeners' school. Growing up in East Lansing, Michigan, where his father was a professor of animal husbandry at Michigan State College, Anderson received his undergraduate degree there in 1918. In 1931 he returned to Harvard's Arnold Arboretum as arborist for four years, and then explored the Balkans in 1934–1935 to collect horticulturally promising strains of ivy, boxwood, and holly. He returned to the Garden in 1935 as geneticist and in a few years was also the Engelmann Professor of Botany at Washington University. Moore had high regard for Anderson's abilities, and recognition was to come to Anderson for his innovative research on plant hybridization and evolution. He

FIGURE 9. Edgar Anderson in 1950, a few years before becoming director of the Missouri Botanical Garden. Photograph by George Dorrill Photographers. (From the archives of the Missouri Botanical Garden.)

described himself as "blunt and unconventional," a description with which most agreed. He was an outstanding and original thinker. As Ledyard Stebbins wrote, "No plant scientist known to me was more able then Edgar Anderson to compare in their natural habitat the leaves, flowers, and wonderfully symmetrical architecture of plants and to express their interrelationships in a meaningful way."[45]

Although Anderson had become the assistant director in 1951, even earlier he had taken particular interest in the horticultural aspects of the Garden and Arboretum by working with garden clubs and other special interest groups. By temperament and desire he was ill-suited to be an administrator. However, he and some of the Trustees believed that the Garden needed new direction, so he reluctantly agreed to be director for a while. With Cutler's help he tried to revitalize the Garden's programs. In the process of trying to make rapid changes, he managed to alienate many of the older staff members. Robert Woodson, who had been the curator of the herbarium since 1948 and coordinator of the *Flora of Panama* and had pushed the building up of African collections, retreated to the university and disassociated himself from the herbarium administration. Carroll Dodge was upset by the sale of the fungi collections and the transfer of portions of the library and came less and less to the Garden. A number of senior Garden and Arboretum employees either left or were unhappy with the changes. These changes included moving the orchids back to the Garden with elimination of many duplicates, and the dismantling of the greenhouses at the Arboretum. A part of the Garden's land on Magnolia Avenue was given to the National Council of State Garden Clubs to build its headquarters. A strong emphasis was given to involving garden clubs and interested amateurs in helping the Garden in practical and monetary ways. Physical plant improvements were pushed and a National Science Foundation grant was obtained to improve the herbarium and library facilities.[46] Fern specialist Rolla M. Tryon, who came in 1948 as the assistant curator of the herbarium and associate professor at Washington University, organized a small systematics symposium for faculty and students of midwestern institutions in 1953.[47] The following year, this was expanded with the help of a National Science Foundation grant, and the annual symposium became a tradition.

Progress was slow and attendance at the Garden did not begin to increase until 1956. Because of ill health and frustration with administrative procedures, Anderson soon resigned to become Curator of Useful Plants and spend his time with his beloved research and teaching. He continued to be awarded research grants and recognitions, including the prestigious Darwin-Wallace Medal from the Linnean Society of London in 1958. The Board was now searching for a decisive leader to be director.

Frits Warmolt Went, California Institute of Technology Professor, Director of the Earhart Laboratory Phytotron, which he helped design, and eminent botanist, was selected to be director in

FIGURE 10. Frits Warmolt Went inside the Climatron while director of the Missouri Botanical Garden, about 1969. Photograph by Arthur Fillmore. (From the archives of the Missouri Botanical Garden.)

1958.[48] At the time he wanted to take a short leave from Cal Tech, and the Garden directorship offered him an opportunity to try out some of his ideas about botanical garden functions. He had impressive international experience with botanical gardens, having grown up in one in Utrecht, where his father was director and where he did his doctorate on pioneering studies of plant hormones. He had been associated some years with the Royal Botanical Garden in Bogor, Java, and had connections with several West Coast United States gardens. An urgent need in St. Louis was the replacement of large deteriorating greenhouses, a challenge that especially intrigued him.

Went believed that the Garden's prime aim was to develop a public awareness of plants by innovative educational displays. By doing this, public support and interest would be assured and would help to develop an increased research program. At first Went had thought that the research should be done at the University, but soon decided that some research should be done at the Garden in a future new building.

In the five years of his directorship, most of Went's efforts went into implementing this plan. At the suggestion of the firm of Murphy and Mackey, a greenhouse in the form of a Buckminster Fuller geodesic dome was decided upon rather than a traditional greenhouse. From his previous experiences, Went knew that many tropical plants needed summer cooling to do well in a greenhouse. Thus, air conditioning as well as heating was needed to provide year-round temperature control. Went named the new greenhouse the "Climatron," because the dome could allow several types of tropical climates by gradient conditions of temperature and moisture. The Climatron, opened in October 1960, sparked much public interest and attracted large paying crowds. (Fig. 10). It served to educate the public on aspects of plant growth under varying conditions, even though the anticipated climatic conditions were not completely controllable. As a building, it received international recognition for its design and concept.[49]

With the aid of Board President Robert Brookings Smith, and the help of the Friends groups, substantial contributions were received to help build the Climatron and to make other improvements. Other innovations were made: several concerts were held; East Indian food was served at a food stand; and special programs in botany for children were instituted. Exotic plants, particularly orchids, were obtained by Went on his many travels.

After a while, Went envisioned making the Garden the cultural center of St. Louis. It was to be a floral pavilion with places for musical events, theater, art, lectures, and restaurants. The city was considering a new cultural center development and thus the Garden became a contender for the site.[50] Some Trustees did not believe that this was an appropriate function for the Garden, nor did they think it affordable. Disagreement led to the resignation of the Board president, even as the City Planning Commission put the Garden fourth on its list of favored sites for a cultural center. Eventually frustration led Went to resign in 1963. Earlier he had begun to obtain funding for a new research building, but much more money was still needed.[51]

Went had revitalized the Garden in the eyes of the public. He had drawn attention to its potential as a cultural force in St. Louis. However, he had not been as able an administrator nor as successful in promoting research as he wanted. The Board of

Trustees was now suspicious of grandiose plans for future deficit development and sought the assistance of outside scientific reviewers for guidance.

In 1965 David M. Gates (Fig. 11) became its new director after two years of indecisiveness and deteriorating research at the Garden. Gates, trained as a physicist but interested in nature since childhood, was in 1965 well known for his original program of applying physics to ecological problems. He had recently become Professor of Natural History at the University of Colorado, a position especially designed for his unique qualifications. Gates was an outstanding scientist who had administrative experience with the American Embassy and the Office of Naval Research in London. He felt that the Garden needed firm direction to overcome the deteriorating horticultural and research programs. He believed that his ecological knowledge would be useful as a research direction for the Garden.[52]

Born a midwesterner, with all of his degrees from the University of Michigan, Gates seemed able to understand St. Louis better than Frits Went had. His first goals were to reestablish credibility with the Board, to promote fiscal responsibility and a balanced budget, to seek new sources of funding, and to rebuild the research and graduate programs at the Garden. With his assistant, Mark Paddock, he was able in his six years of directorship to achieve these interconnected goals. He instituted a general admission charge. He hired new researchers and staff. With their help, he was able to obtain grants for support of Garden activities. He initiated a $3 million Capital Fund Drive to help fund a new herbarium and library building, make other improvements, and obtain a development plan. In his first three years he had increased the total staff by 50%, and the scientific staff by 200%.[53] Budgets had been balanced each year. Research in systematics had been revitalized by the new Director of the Herbarium, Walter H. Lewis, and the new Curator of Cryptogams, Marshall R. Crosby. Grants were obtained for support of herbarium and library improvements and for significant research. A major grant was obtained to help with the construction of a new herbarium and library building, to be named the John S. Lehmann Building, which was completed in 1972. The herbarium passed its two millionth specimen mark, and the *Flora of Panama* project was moving ahead with new and old staff, including John D. Dwyer, a professor at St. Louis University, who had been involved since Woodson's time. A new herbarium and library were established in the Panama Canal Zone as well.[54]

FIGURE 11. Director David Murray Gates measuring the temperature of a rose at the Missouri Botanical Garden. Photograph by Claude Johnston. (From the archives of the Missouri Botanical Garden.)

The Gates administration was to write that "The inertia gripping this institution for the last 30 years has been overcome. We have taken positive steps to fulfill our proper role in this community and in the significant world."[55] Optimism was returning to the staff and all seemed on track when Gates left to become director of the University of Michigan's Biological Station in 1971. He had built up a large, funded, biophysical ecology program at the Garden and Arboretum. This sort of ecological research was to leave with Gates, at the same time that the revitalized systematics program was to persist and grow when systematist Peter H. Raven came immediately to become director.

Raven (Fig. 12) who grew up and went to school in California, was an outstanding young botanist teaching at Stanford University. He had diverse interests in systematics, ethnobotany, ecology, evolutionary biology, and general natural history.[56] In the 18 years of Raven's directorship, with the help

FIGURE 12. Peter Hamilton Raven shortly after becoming the director of the Missouri Botanical Garden. (From the archives of the Missouri Botanical Garden.)

of his wife Tamra, and for some years of William Klein, the Garden has moved forward on many fronts. Some new focus gardens were designed: an English woodland garden; a new rose garden, and a Japanese garden. These, together with expanded floral displays, added outdoor sculptures, and special events have quadrupled attendance since 1971, resulting in more than 800,000 visitors a year with a staff of about 250 people. The Ridgway Center, a new entrance building containing various facilities and the public education programs, opened in 1982. The Lehmann Building was renovated in 1987 to make it more useful for its growing herbarium and library functions.[57] The Climatron is being renovated with glass replacing plexiglass and should reopen next year. [The Climatron did reopen in March 1990.]

It is the area of research, particularly in systematics and tropical ecology, where the Missouri Botanical Garden has taken leadership. With a scientific staff of about 40 scattered throughout the world, and a herbarium of 3.6 million specimens, the Garden has accomplished much. It has been able to receive tax support for the first time, which together with an expanded volunteers program, allows it to do much. It continues to have a significant interest in the flora of Central America, particularly Panama and Nicaragua, and be a major focus for the *Flora Mesoamericana* project. It has been investigating the South American floras, particularly those of the northern part. Africa, particularly the rapidly changing flora of Madagascar and southern Africa, has been an interest of the Garden for many years and continues to engage researchers. The North American flora project is now housed at the Garden, and a new flora of China project is developing. Very active research continues on bryophytes and ferns. The Garden is a major center for study of the plant kingdom at the organismal and higher levels. Went, Gates, and Raven have been actively involved in national and international botanical activities.[58]

So we come to the end of this brief history of the Missouri Botanical Garden. The eccentric essayist-historian Lytton Strachey once wrote that "ignorance is the first requisite of the historian,"[59] because the historian must be selective and interpretive and must ignore much. Perhaps it would be more accurate to say that the historian is more like a maker of myths, myths that have one or more morals. What then is the mythology of the Missouri Botanical Garden? In my view, one moral is that an institution with a divided administrative structure, Board and Director, can thrive, though at times there may be strong conflicts. Another moral is that a botanical garden, with strong traditions, can be an effective force for good in a community and in society. The Missouri Botanical Garden, for example, has helped to beautify St. Louis, and helped to clean up its air, has educated Missourians about their natural and horticultural heritage, and has helped expand people's view of the importance of vegetation for human survival. It has shown that botanical and horticultural research can be made meaningful to the general public.

I have reviewed how the founder and six directors, each with differing views of its mission but all concerned with education and research, have molded the Garden. The ordinary citizen and the scientific community have been educated in the importance of the Garden's research, whether it be through a flora of Missouri or Panama, a new hybrid water lily, an understanding of the genetics of significant crop plants, an experiment with an ecologically designed greenhouse, or a race to know the plants of the disappearing tropical rainforests. The mythology of the Missouri Botanical Garden

is one that is real, perhaps more real than fact or history.

NOTES

4. Henry Shaw manuscripts, M.B.G. archives, box 3 of botanical manuscripts, 1876 or later, beginning "American Trees."
5. The best source of information about Shaw is the recent biography by William Barnaby Faherty, S.J., *Henry Shaw, His Life and Legacies*, Univ. Missouri Press, Columbia, Missouri, 1987, 228 pp. Other useful sources are: Thomas Dimmock, "Henry Shaw, a biographical sketch," [*Annual Report*] *Missouri Botanical Garden* [1st], St. Louis, 1890, pp. 7–28. (Reprinted as pamphlet n.d. but probably late 1930s, 30 pp.); E[dgar] A[nderson], "Henry Shaw—a pictorial biography," *M.B.G. Bull.* 42: 103–118, 1954; Edgar Anderson & Dorothy Brockhoff, "Henry Shaw, a pictorial biography," *M.B.G. Bull.* 55(6): 1–16, 1967; and Jean Marie Denken & James R. Reed, "Henry Shaw, his life and legacy," [unpaged pamphlet, M.B.G., St. Louis] n.d. (probably 1977).
6. For example, see: N. S. B. Gras, "An early sedentary merchant in the Middle West, records available for a study of the career of Henry Shaw," *Bull. Business History Soc.* 18: 1–9, 1944; Dana O. Jensen, "The enigma of Mr. Shaw," *Missouri Historical Soc. Bull.* July 1959, pp. 311–318; James Neal Primm, "Henry Shaw, Merchant Capitalist," *Gateway Heritage* 5(1):2–9, 1984; and Faherty, 1987.
7. The literature on the history of botanical gardens is extensive. A few examples are: Wolfgang Born, "Botanical gardens," *Ciba Symposia* 11: 1093–1124, 1949; Frans Verdoorn, "Botanical gardens and arboretums of the past and their reconstruction," *Annee Biol.* 29: 275–282, 1953; W. B. Turrill, *The Royal Botanic Gardens Kew; Past and Present*, Herbert Jenkins, London, 1959, 256 pp.; William Thomas Stern, "Botanical gardens and botanical literature in the eighteenth century," *in* Allan Stevenson (compiler), Catalogue of Botanical Books in the Collection of Rachel McMasters Miller Hunt, 2(1): xli–cxl, 1961; Edward Hyams, *Great Botanical Gardens of the World*, Macmillan Co., New York, 1969, 288 pp.; H. R. Fletcher & W. H. Brown, *The Royal Botanic Garden, Edinburgh, 1670–1970*, H.M. Stationery Office, Edinburgh, 1970; C. D. Darlington, "The Oxford Botanic Gardens: 1621–1971," *Nature* 233: 455-456, 1971; W. T. Stern, "Sources of information about botanic gardens and herbaria," *Biol. J. Linnean Soc.* 3: 225–233, 1971; Wilfrid Blunt, *In For a Penny; a Prospect of Kew Gardens: Their Flora and Falballas*, Hamish Hamilton, London, 1978, 218 pp.; and A. D. Boney, *The Lost Gardens of Glasgow University*, Christopher Helm, London, 1988, 298 pp. Information about the garden at Padua can be found in: David W. Lee, "Padua," *American Horticulturist* 59(4): 18–21, 1980; and Lucia Rossetti, *The University of Padua; an Outline History*, Trans. A. W. M. Hargraves, Edizioni Lint, Trieste, 1983, 75 pp.
8. See, for example: Philip C. Ritterbush, *Overtures to Biology; the Speculations of Eighteenth Century Naturalists*, Yale Univ. Press, New Haven, 1964, 287 pp.; Lorin Anderson, "Charles Bonnet's taxonomy and chain of being," *J. Hist. Idea* 37: 45–58, 1976; John Prest, *The Garden of Eden; the Botanic Garden and the Recreation of Paradise*, Yale Univ. Press, New Haven, 1981, 122 pp.; and Janet Browne, *The Secular Ark; Studies in the History of Biogeography*, Yale Univ. Press, New Haven, 1983, 273 pp.
9. Letters from Shaw to Hooker in 1856 and 1857 are in the archives of the Royal Botanic Gardens Kew (Book 64) and from Hooker to Shaw in 1857 and 1858 are in the archives of the Missouri Botanical Garden (Director's Office Scrapbook 1857–1890).
10. Shaw letter to Hooker, Aug. 10, 1886 (Book 64, # 360).
11. Some examples are: "Sir William, kind, active and strong as he is, promises to do any thing for your establishment you may desire, by advise [sic] and by sending seeds and plants suited for our climate and in any other way. He seems to take much at heart this business, and hopes that you will be able to establish a model botanic and agriculture garden, and Herbarium and Museum in the centre of North America." G. Engelmann to H. Shaw, Kew, Aug. 11, 1857 (M.B.G. archives, Director's Office Scrapbook 1857–1890); "As your endowment is quite unprecedented in this country, if not anywhere, at least in extent and capabilities, I was naturally anxious in respect to its plan and its prospects. You know from conversation what my ideas and my hopes are for its future, and that I am very confident of its complete success and enduring usefulness." A. Gray to H. Shaw, Cambridge, May 29, 1884 (M.B.G. archives, Director's Scrapbook 1857–1890); "Mr. Shaw took me into his counsel and, without going here into details, without seeing a chance for doing much while Mr. Shaw lives, which cannot be very long, I see there is a great opportunity coming, and I think that none of the provisions he has made will hinder the right development of the Mississippian Kew, which will hardly be 'Kew in a corner.' And if he follows my advice and mends some matters, there will be a grand foundation laid." A. Gray to J. D. Hooker, Cambridge, June 9, 1884, *in* Jane Loring Gray (editor), *Letters of Asa Gray*, Boston, 1894, p. 753.
12. "Another thing that I have at heart is the offer that has been made of an excellent and very rich Herbarium, that of the late Prof. Bernhardi at Erfurth. It can be had now for something like 600 dollars and has cost more thousands (—they tell me of 8–10,000 dollars) to amass. Application ought to be made soon.—What do you think of this trifle of $600 for such a treasure—and what of the sum for a library?" G. Engelmann to H. Shaw, Kew, Aug. 11, 1857 (M.B.G. archives, Director's Office Scrapbook 1857–1890). See also: *Trans. Acad. Sci. of St. Louis* 1: 316, 1856–1860; "Early collections in the Garden herbarium," *M.B.G. Bull.* 7: 29–35, 1919; and William G. D'Arcy, Mysteries and treasures in Bernhardi's herbarium," *M.B.G. Bull.* 59(1): 20–25, 1971.
13. A photograph of Henry Shaw lying in state in the Museum is in the M.B.G. archives and is reproduced in *Gateway Heritage* 5: 9, 1984; ". . . no attempt can be made to form a museum and the specimens collected by Mr. Shaw for the purpose have suffered to such an extent as to be for the most part worthless, owing to the ravages of insects and the accumulation

of dust during many years." *2nd Ann. Report M.B.G.*, p. 25, 1891.

14. The earliest published guide to the Garden was that of 1893, *Missouri Botanical Garden*, Board of Trustees, [St. Louis], 9 pp., 11 pls., 1 folding map. Other guides were published as they were revised at later dates.
15. D. H. MacAdam, *Tower Grove Park of the City of St. Louis*, R. P. Studley & Co., St. Louis, 1883, 119 pp.; T. V. Brumfield, "A study of philanthropy: Tower Grove Park," *Missouri Historical Soc. Bull.* 21: 315–322, 1905; [D. H. MacAdam], "Tower Grove Park. A careful review of its foundation and history," *The Republic*, June 26, 1890; "Shaw's living legacy: Victorian grandeur and modern fun mix," *M.B.G. Bull.* 64(8) u.p., 1976; and Robert E. Knittel, *Walking in Tower Grove Park, a Victorian Strolling Park*, 2nd edition, Grass-Hopper Press, St. Louis, 1983, 105 pp.
16. "Henry Shaw's will. Admitted to Probate at St. Louis, Sept. 2, 1889." [*1st*] *Ann. Report* M.B.G., pp. 29–55, 1890; this has been reprinted in pamphlet form over the years, the latest printing being: *The Will of Henry Shaw Establishing the Missouri Botanical Garden and Other Documents Pertaining Thereto*, M.B.G., St. Louis, 1986, 45 pp.
17. "An act to enable Henry Shaw to convey or devise to trustees certain lands." (Reprinted from Missouri Sessions Acts of 1859, p. 434) [*1st*] *Ann. Report M.B.G.*, pp. 26–28, 1890.
18. *Ibid.* p. 26.
19. *Ibid.* pp. 36–37.
20. No definitive biography of Trelease is available. The best published sources are: L. H. Pammel, *Prominent Men I Have Met, III, Dr. William Trelease*, the Author, Ames, Iowa, 1927, 84 pp.; J. Christian Bay, *William Trelease 1857–1945, Personal Reminiscences*, the Author, Chicago, 1945, 12 pp.; J. T. Buchholz, "William Trelease 1857–1945," *Science* 101: 192–193, 1945; J. M. Greenman, "William Trelease," *M.B.G. Bull.* 33: 71–72, 1945; Louis Otto Kunkel, "William Trelease, February 22, 1857—January 1, 1945," *Biographical Memoirs, National Academy of Sciences of the United States* 35: 307–332, 1961; and Joseph Ewan, "Trelease, William," *in* C. C. Gillespie (editor), *Dictionary of Scientific Biography* 13: 456, Charles Scribner's Sons, New York, 1976. The papers of Trelease are in the archives at Cornell University and the University of Illinois. An extensive bibliography is found in Kunkel, 1945. The only negative assessment of Trelease known to me is by Marcus E. Jones: ". . . I am compelled to say that in my judgment he has no scientific judgment and is utterly unfit to monograph any genus . . . ," quoted in Lee W. Lenz, *Marcus E. Jones, Western Geologist, Mining Engineer and Botanist*, Rancho Santa Ana Botanic Garden, Claremont, 1986, p. 205 (I thank Joseph Ewan for calling my attention to this).
21. Much has been written about the Fair. Some examples are: *The Greatest of Expositions, Completely Illustrated. Official Publication*, Official Photographic Company of the Louisiana Purchase Exposition, St. Louis, 1904, 288 pp.; Margaret Johanson Witherspoon, *Remembering the St. Louis World's Fair*, Comfort Printing Co., St. Louis, 1973, 96 pp.; and James Neal Primm, *Lion of the Valley, St. Louis, Missouri*, Pruett Publishing, Boulder, Colorado, 1981, pp. 401–418.
22. *Missouri Botanical Garden*, Board of Trustees, St. Louis, 1904, p. 3.
23. *16th Ann. Report M.B.G.*, 1905, p. 20.
24. The figure for Shaw's botanical library can be obtained from a manuscript "Catalogue of Books belonging to the Library of the Mo. Bot. Gardens" written by J. Monell probably about 1876, and from the inventory of the Town House and Tower Grove House prepared at Shaw's death, both in the M.B.G. archives; *3rd Ann. Report M.B.G.*, 1892, pp. 15–16; *16th Ann. Report M.B.G.*, 1905, p. 23; and Board of Trustees' Minutes, Apr. 10, 1912 (M.B.G. archives).
25. [J. C. Bay], "The Sturtevant prelinnean library," *7th Ann. Report M.B.G.*, 1896, pp. 123–209; C. E. Hutchings, "A supplementary catalogue of the Sturtevant prelinnean library," *14th Ann. Report M.B.G.* 1904, pp. 233–316; Board of Trustees' Minutes, May 14, 1902 (M.B.G. archives).
26. Board of Trustees' Minutes, Dec. 14, 1904 (M.B.G. archives).
27. For further information about von Schrenk, see: Board of Trustees' Minutes, Mar. 9, 1904; Apr. 12, 1905; June 12, 1907; (M.B.G. archives); Guy Forshey, "Interesting St. Louisians, Dr. Hermann von Schrenk," *St. Louis Post-Dispatch*, Oct. 20, 1929, p. 5, 9; August P. Beilmann, "Hermann von Schrenk (1873–1953)," *M.B.G. Bull.* 41: 50–53, 1953; and James E. Cronin, *Herman von Schrenk: The Man Who was Timber, a Biography*, Kuehn, Chicago, 1960, 257 pp.
28. ". . . have you got a man to spare—or do you know of a man—a practical man—gardener—tree-fancier—&c &c who could come and take charge of things. If you can light on a man with botanical knowledge enough, and get a *worker*—very well. If not I suppose we must have a botanical assistant here, to do what I have always to do—If we could put all in one, so much the better. If you cannot supply us—I have a Yankee Gardener in view, who for practical work might answer." A. Gray to J. D. Hooker, Cambridge, Dec. 27, 1871 (Asa Gray Kew Correspondence 1839–1873, Royal Botanical Gardens, Kew, archives).
29. Board of Trustees' Minutes, Feb. 10, 1904; May 11, 1904, Nov. 9, 1904 (M.B.G. archives); *16th Ann. Report M.B.G.*, 1906, pp. 29–30.
30. Board of Trustees' Minutes, Nov. 9, 1904; Jan. 11, 1905 (M.B.G. archives).
31. "The work *has* been hard and uphill, but I hope that the results are really worth all it has cost me. There never has been a time when the Board has not been pretty equally divided between concentrating everything on decorative gardening and allowing me to make modest advances along the whole front of Henry Shaw's plan, but the late President, Mr. Lackland, had confidence in the plan and my ability to make the limited revenue do the wise thing to such an extent that scarcely a dissenting vote has been recorded on anything, and about four years ago my salary was increased with expression of the belief that my withdrawal would set the establishment back for years and that there was no dissatisfaction with me or opposition to my policies that would warrant me in considering leaving the Garden if tempted to

do so. A new ruler has arisen in Egypt, who knoweth not Joseph, since Mr. Lackland's death, and a year ago the new President advised me that 'we're going to have more garden and less science, now' and that I should have to do a good deal of talking to bring him to agree with my suggestion that I would rather have him say 'more garden but no less science.' I did not tender my resignation then, for I felt that it would be wrong to abandon my part on such a proposition unless it were strongly enough based as to make further struggle hopeless. There is no question, though, now that I've opened a jack pot on queens but the President has four acres; but, as I told him, I'm enough of a sportsman not to whimper for my chips or to shoot up the room and bring the police down on the game. The outcome will probably be a quiet withdrawal without defamation of character on either side—which is what I want, for the procedure is common enough in business management and not attended by the resentment and sentiment that University changes in administration usually bring out." W. Trelease to W. Farlow, St. Louis, Feb. 16, 1912 (Farlow Library and Herbarium, Harvard University, Farlow papers).

32. "Hunting orchids in the Andes for St. Louis has its trials," *St. Louis Post-Dispatch*, Aug. 26, 1923, pp. 7, 14; "Brief biographies, George H. Pring," *The Aquarium*, Aug. 1945, pp. 65–66; "George H. Pring retirement issue," *M.B.G. Bull.* 51(2): 1–12, 1963; Olivia Skinner, "The three loves of George Harvey Pring," *St. Louis Post-Dispatch*, Jan. 3, 1963; George H. Pring, "The Garden as laid out by Henry Shaw," *M.B.G. Bull.* 52(5): 1–12, 1964; Edgar Anderson, "Learning from the bees: G. H. Pring and water-lily breeding," *M.B.G. Bull.* 54(10): 8–10, 1966; and "George H. Pring 1885–1974," *M.B.G. Bull.* 63(5): 1–2, 1974.
33. "Tropical Life friend, no. 315, Dr. George T. Moore," *Tropical Life*, Sep. 1931, pp. 170–171; E[dgar] A[nderson], "Dr. George T. Moore, Director 1913–1953," *M.B.G. Bull.* 44: 141–142, 1956; and Carroll W. Dodge, "George Thomas Moore (1871–1956)," *Amer. Philos. Soc. Yearbook 1957*: 145–148, 1958.
34. Board of Trustees Minutes, Mar. 13, 1912 (M.B.G. archives).
35. Board of Trustees Minutes, Jan. 13, 1915 (M.B.G. archives).
36. Board of Trustees Minutes, Feb. 13, 1918; Oct. 17, 1928 (M.B.G. archives).
37. *Missouri Botanical Garden Illustrated* Board of Trustees of the Missouri Botanical Garden, [St. Louis] n.d. [ca. 1926], [56 pp.], folding map; and George T. Moore, "Thirty eighth annual report of the Director," *M.B.G. Bull.* 14(1): 1–22, 1927.
38. "Young St. Louisian writes book on 1400 flowers of Missouri," *St. Louis Globe-Democrat*, Apr. 22, 1940; Cora Steyermark, *Behind the Scenes*, Missouri Botanical Garden, St. Louis, 1984, 158 pp; George Yatskievych & Luther J. Raechal, "In memoriam—Julian Alfred Steyermark, 1909–1988," *M.B.G. Bull.* 77(1): 5, 1989; Scott A. Mori & Brian M. Boom, "In memoriam—Julian A. Steyermark (1909–1988), *Bull. Torrey. Bot. Club* 116: 75–76, 1989; and [Julian Steyermark], "Steyermark Recollections," *Annals M.B.G.* 76: 627–651, 1989.
39. Board of Trustees' Minutes, Mar. 17, 1926 (M.B.G. archives); and John D. Dwyer, "The history of plant collecting in Panama," *in* William G. D'Arcy & Mireya D. Correo A. (editors), *The Botany and Natural History of Panama: La Botanica e Historia Natural de Panama*, Monogr. Syst. Bot. Missouri Bot. Gard. 10: 179–183, 1985.
40. Marilyn M. LeDoux, "Missouri Botanical Garden and its orchid collection," *Amer. Orchid Soc. Bull.* 58: 553–558, 1989; and Marilyn M. LeDoux, "Orchids through the years at the Missouri Botanical Garden," *Amer. Orchid Soc. Bull.* 58: 696–702, 1989.
41. "Smoke to cost city at least part of Shaw's Garden," *St. Louis Post-Dispatch*, Feb. 21, 1923; Board of Trustees' Minutes, Mar. 21, 1923; Feb. 18, 1925 (M.B.G. archives); "When 'Old Sol' smiles or ducks under the clouds it is recorded at Shaw's Garden," *St. Louis Globe-Democrat Sunday Magazine*, Aug. 17, 1930; and Board of Trustees' Minutes, June 5, 1940 (M.B.G. archives).
42. Board of Trustees' Minutes, Jan. 18, 1933 (M.B.G. archives).
43. *M.B.G. Bull.* 44: 142, 1956.
44. "Men of science in St. Louis, world famed botanist seeks clue to civilization's origin of corn," *St. Louis Post-Dispatch*, Feb. 8, 1948; Hugh Cutler, "Plants, man, life and Edgar Anderson," *M.B.G. Bull.* 57(5): 305, 1969; and John J. Finan, "Edgar Anderson 1897–1969," *Annals M.B.G.* 59: 325–345, 1972.
45. Charles B. Heiser, Jr., "Student days with Edgar Anderson, or how I came to study sunflowers," *Annals M.B.G.* 59: 362–372; G. Ledyard Stebbins, "Edgar Anderson: recollections of a long friendship," *Annals M.B.G.* 59: 373–379; and interviews with William L. Brown, M. Donald Duvick, and G. Ledyard Stebbins, 1989 (tapes in M.B.G. archives).
46. Interview with Hugh Cutler, 1988 (tape in M.B.G. archives).
47. Interview with Rolla and Alice Tryon, 1989 (tape in M.B.G. archives).
48. "Frits Went, California botanist, named Shaw's Garden director," *St. Louis Post-Dispatch*, May 18, 1958; transcripts from Went's diaries of the period and an interview of 1988 are on file in the M.B.G. archives.
49. "The Climatron opens to the public," *M.B.G. Bull.* 48: 131–133, 1960; "And suddenly last summer," *Progressive Architecture*, Apr. 1961, pp. 174–178; George McCue, "The Climatron as architecture," *St. Louis Post-Dispatch*, Apr. 30, 1961, p. 5B; "The Climatron," *A[mer.] I[nstitute] [of] A[rchitects] Journal*, May 1961, pp. 27–32; Judith Jenkins, "A greater Shaw's Garden, Director Went envisions many future innovations," *St. Louis Globe-Democrat*, Nov. 24, 1962; and Robert Dingwall & Barbara Lawton, "The Climatron, Missouri Botanical Garden's space age greenhouse," *M.B.G. Bull.* 58(4): 12–21, 1970.
50. "Program of music at Shaw's Garden," *St. Louis Post-Dispatch*, Sep. 23, 1959; "Where to put a cultural center," *St. Louis Post-Dispatch*, Jan. 8, 1963; "Downtown gets preference for culture center," *St. Louis Post-Dispatch*, Jan. 20, 1963; and "The cultural center reports," *St. Louis Post-Dispatch*, Jan. 27, 1963.
51. Frits W. Went, "Missouri Botanical Garden, report of the director for 1962," *M.B.G. Bull.* 51(3): 1–

8, 1963; Frits Went, diary Apr. 1, 1963 and other diary entries (M.B.G. archives).

52. Edgar Anderson, "David M. Gates, the new director," *M.B.G. Bull.* 53(9): 1–7, 1965; Robert W. Stock, "Saving the world, the ecologist's way," *New York Times Magazine*, Oct. 5, 1969; and Gates interview 1988 (M.B.G. archives).
53. Mark Paddock, "Foreword," *M.B.G. Bull.* 57(1): 1, 1969; and Mark Paddock, "Annual report — 1969, a significant decade," *M.B.G. Bull.* 58(2): 2–4, 1970.
54. Thomas B. Croat, "The Missouri Botanical Garden in Panama," *M.B.G. Bull.* 60(1): 19–22, 1972.
55. Paddock 1969; and "The John S. Lehmann Building, a new era for the Missouri Botanical Garden," *M.B.G. Bull.* 60(3): 6–12, 1972.
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ONE HUNDRED YEARS OF PLANT TAXONOMY, 1889–1989[1]

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ABSTRACT

One hundred years ago taxonomic botany was at the end of the first phase of producing great regional floras and encyclopedic compendiums, especially with the work of George Bentham and Joseph Hooker in Britain, Asa Gray in the U.S.A., and Alphonse de Candolle in Switzerland. The vast influx of new botanical discoveries from exploration had highlighted interest in biogeography, interpreted in terms of new evolutionary insights. The subject had been in high regard and major herbaria had recently been founded. A widespread decline of activity and prestige followed, when emphasis shifted to other botanical fields, except in Germany where Adolf Engler further developed encyclopedic coverage of plant families and genera worldwide. Revival of biological taxonomy came slowly through genetics to the "new systematics." Karyology, biosystematics, phytochemistry, and comparison of isozymes were in turn seen as panaceas; each failed to meet these expectations but continues to contribute as part of the armory of relevant approaches. Emphasis on methods of analysis led to the decade of numerical phenetics. Partly from lack of a satisfactory theoretical basis, phenetics came to be widely rejected but gave place to cladistics, ranging from the avowedly phylogenetic to abstract pattern analysis. Macromolecular genetics with analysis of data from nuclear, ribosomal, mitochondrial, and especially chloroplast genes is now rapidly producing robust data to address many previously intractable problems at all taxonomic levels by selection of appropriate gene systems. Such data may produce convincing phylogenetic trees without input from morphology, leading some to question whether systematic botany remains "an unending synthesis," though warnings against overconfidence have been sounded both from aspects of gene systems and from the way the data are analyzed. A challenge is to maintain cohesion in systematics so that the new developments are a scientific stimulus to the subject as a whole and so that herbaria and other institutions concerned with floristic projects remain within the mainstream of scientific taxonomy. Insofar as macromolecular systematics lives up to its early promise, the task of systematics may eventually become, in part, the interpretation of morphology and evolution in terms of highly corroborated phylogenies—a synthesis on new terms. As well as these more theoretical approaches, providing organized information on the diversity of the world's plants through national and regional floras remains a priority.

A brief paper cannot adequately review a century of work by taxonomists, who were numbered in tens a century ago and who are now in thousands. Their work filled our herbaria with specimens and our libraries with publications. This whirlwind tour places emphasis on the beginning and end of our time frame, and gives least attention to those fields where my lack of expertise would otherwise be most conspicuous. Two other limitations will be apparent. The extent of emphasis on work in the English-speaking countries and on seed plants alone is justified by my greater familiarity with those areas.

AN UNENDING SYNTHESIS?

With this eloquent and much-quoted phrase Lincoln Constance (1964) characterized the nature of systematics—a term that I use in part interchangeably with taxonomy (in general agreement with Small [1989] in the use of these terms). Modern macromolecular genetics has contributed such powerful tools to taxonomy that Gottlieb (1988) queried whether this characterization was still appropriate, and I will return later to this question. Traditionally, data from many fields have been grist for the mill of taxonomy. So this subject has reason to be responsive to developments in science generally, as well as profiting from technological advances that increase its power to assemble and organize relevant data. This responsiveness has been and remains a two-way process. Taxonomy has given the basis for one of the greatest unifying concepts in science—evolution—since it is taxonomy that has the main task of making accessible our organized knowledge of the patterns of diversity of living things.

A hundred years ago the scientific context for

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taxonomy was the result of a century of dramatic progress (e.g., Taton, 1965). Since the start of the nineteenth century there had been:

—the acceptance of atomic theory with insight into molecular structure and chemical reactivity;
—bacteriology with the inception of scientific medicine;
—the interpretation of geological structures, with the international geological scale of epochs and periods replacing "catastrophic" models of the earth's past;
—the beginning of understanding of the structure of organisms in terms of cells, nuclei, cell division, and life cycles;
—and then, most dramatic in modifying general thought, had been the concept of biological evolution.

Still lacking were:

—extension of the limits of knowledge of the universe in its largest extent that would come with modern astronomy and cosmology and in its fine detail extending from modern microscopy to quantum physics;
—modern philosophy of science with sharper focus on falsifiability of hypotheses;
—systems theory and now chaos theory;
—sophisticated concepts of energy, matter, and their range of manifestations and transformations in physical and biological systems;
—plate tectonics and the history of continental movements and paleoclimatology;
—the localization of genetic inheritance largely to chromosomes, with concepts of genes and mechanisms of heredity;
—classification and definition of the major categories of organisms beyond simplistic groupings into plants, animals, and fungi;
—the symbiotic theory of the eukaryotic cell;
—technical advances in all fields, including chemical analysis, microscopy, computing, and communication;
—extension of centers of scientific research and teaching beyond the limits of Europe and North America.

End of an Era

A century ago Charles Darwin had been dead seven years and the appearance of *The Origin of Species* was 30 years into the past. What scientist then would have thought that evolution (as distinct from 'Darwinism') would still be a contentious issue, still needing to be defended in some circles although not within science, a hundred years into the future? Within science it is evidence of Darwin's importance that his work still attracts critics today, but mostly their concerns are with the nature of the evolutionary process and the way it is described, rather than denying evolution itself.

In the previous century, before 1889, exploring parties in many regions had been gathering specimens of unfamiliar plants, still bringing them to the seats of learning in the temperate northern hemisphere, rather than expecting or seeking to establish expertise distributed worldwide. This pace of botanical exploration and interest in joining expeditions continued to be powerful stimuli in attracting active minds to taxonomic biology, as they had been in the time of Charles Darwin and earlier.

By 1889 taxonomy was at the end of the first round of great regional floras and encyclopedic treatments of the world's plant taxa. George Bentham had died in 1884 and Asa Gray in 1888, although Alphonse de Candolle was still alive and Joseph Hooker would continue publishing for another 22 years till 1911. The importance of these botanists and their work is such that we should extend our time frame back a little to consider them all. Indeed, by going back to September 1880 we could have looked in on any of several little dinner gatherings in the director's house at Kew Gardens near London and found all four of them together (J. Gray, 1893). These were all old friends, old in years and who had met many times before, but think of what a prodigious botanical output is represented here.

First the host to these gatherings, Joseph Hooker. Dr. Hooker was for 20 years director of the Royal Botanic Gardens, Kew, London and spent a long active retirement, his last botanical paper being published in the year of his death at the age of 94 (Allan, 1967; Bower, 1919). He had made notable travels in the southern continents, in India, and high into the Himalayas. The *Flora of British India* and *Genera Plantarum* were joint with George Bentham, who took the greater share, but major essays on plant geography were his alone. The incisive, wide-ranging phytogeographical assessments in his discussion of southern hemisphere plant distributions (Hooker, 1859) were only set aside when modern plate tectonics gave a new framework for interpreting plant geography. Joseph Hooker had played a major part in encouraging Charles Darwin and had been Darwin's closest confidant and first supporter.

Next there is Bentham, known to his associates as a prodigious worker (Jackson, 1906), who had

published a wealth of critical treatments of particular families as well as the *Flora Hongkongensis* and the *Handbook of the British Flora*. His *Flora Australiensis* had been 16 years in preparation, but during those years he had been pressing on also with the mighty *Genera Plantarum*, jointly with Hooker. His botanical judgments have stood well, but subsequent authors have too often simply used Bentham's classifications and ignored his comments that indicate how often decisions were tentative, as seen by himself, and influenced by the limited information available at the time.

Alphonse de Candolle brings yet another strand. He had succeeded his father, Augustin-Pyramus de Candolle (A. P. de Candolle), as professor and director of the botanic garden at Geneva, and also inherited responsibility for the *Prodromus* (A. P. de Candolle, 1824 et seq.). This work attempted a systematic treatment of the world's dicotyledons down to the level of species and variety. The elder de Candolle had turned away from the artificiality of the Linnean system and attempted to apply the modern principles of his time, and his son had reinforced this trend. The *Prodromus* set standards of format and nomenclature that became increasingly widely adopted. After taking over the half-completed work, with only seven of the eventual 17 volumes published, Alphonse made the work more international and better-based through seeking external collaborators, by visiting other herbaria, and through extensive loans of specimens. His publication *La Phytographie* became a standard work on the principles of plant taxonomy, and he had a leading part in the first codification of botanical nomenclature (A. de Candolle, 1867).

Then there was Asa Gray. He had collaborated with John Torrey on *The Flora of North America* (Torrey & Gray, 1838–1843) and later had published widely on the plants and phytogeography of North America and also their relations with the flora of Japan. A notable teacher, he had produced a range of important textbooks, inspired a stream of outstanding botanists, and founded the Harvard herbarium that bears his name. Himself a systematist, he also encouraged students into other disciplines and was conscious of the value and importance of morphology, anatomy, and physiology.

A Time of Change, a Century Ago

Botany as a Scientific Career

The careers and work of these four botanists emphasized changes that were already in evidence and that would set the scene for the future. Botany in the nineteenth century had been both burdened and blessed by being adopted as a socially desirable genteel pursuit for the newly wealthy, and one that combined well with the romantic idealism of the time (Scourse, 1983). This fashion grew as a corollary to increasing industrialization and urbanization and gave the subject some problem in establishing its scientific credentials. But for our group of botanists there was no doubt: their motivation and careers had been scientific.

Hooker and Gray had originally studied medicine, thus receiving some formal botanical training; Bentham and de Candolle had taken law. Two had learned much of their botany assisting distinguished fathers, whereas Gray had worked with John Torrey at New York. We see here two types of botanical inheritance.

Gray received from Torrey inspiration and knowledge and in turn passed this on in equal measure to his many students. The age of the teacher and student was replacing that of the master with his assistant. It was now the time of the professional scientific career. Bentham seemed to regard himself as something of an amateur even when he had major achievements to his name, in contrast to Dr. Hooker and others formally trained in botany. Also, Bentham alone of this group had continued the earlier tradition of the unpaid scholar, having a modest inheritance and "finding . . . that I need not toil for our support [he observes], I determined to give up the law and devote myself entirely to botany" (Jackson, 1906).

The Growth of Collections and Institutions

When William Hooker was appointed as director of Kew Gardens in 1841 it had neither herbarium nor library and was essentially a pleasure garden (Hepper, 1982). He left it as the scientific institution that his son Joseph continued to develop. The original nucleus of the Kew herbarium was William Hooker's personal collection, purchased on his death by the British government (Blunt, 1978; Desmond, 1975). Its library also started with William Hooker's own books, much augmented when Bentham offered his library of 1,000 volumes; Bentham made only the condition that he be allowed to use it there (King, 1985).

That most useful, if simplest, of resources for the taxonomic botanist—the herbarium specimen—already had a long history, but large herbaria were recent developments. The foundation of London's Kew herbarium is dated as 1853, and collections were building up in St. Louis, at Harvard University, and elsewhere. But many other

major herbaria, for example in New York and Chicago, were still in the future. Much of the early contact among botanists arose through requests to collect or identify specimens, as for example Asa Gray's early dealings with John Torrey and later with George Engelmann (J. Gray, 1893; Humphrey, 1961). Now that there are large herbaria of worldwide scope widely distributed, it is hard to equal the enthusiasm with which these botanists awaited and received new consignments of specimens from distant lands.

None of these four great men had successors of comparable standing. Geneva continued as an important botanical center but never again rivaled its place in the time of the de Candolles. Similarly, after the death of Asa Gray, no individual has dominated the American botanical scene as he had (Ewan, 1969; Heiser, 1969), although important successors included Charles Bessey, notable for his attempt at a phylogenetic system of flowering plant classification, and Liberty Hyde Bailey, with his unrivaled works on cultivated plants.

Under the two generations of Hookers, Kew developed exchange, especially in plants of potential economic value, with the British colonies, and Kew directors determined the control of colonial botanical gardens. Under its next director, Thistleton-Dyer, with the British Empire at its peak, economic botany came to dominate much of Kew's work and influence (Brockway, 1979). Kew continued as an outstanding center of botanical resources, but no longer held the lead in botanical research.

DEVELOPMENT OF BOTANICAL PROCEDURES AND COOPERATION

Standardized formats and procedures for plant description, specimen citation, and reference had developed early. Works from this time therefore have formats relatively little different from many modern works. Indeed, some standard conventions in botany seem to be vestigial and probably regrettable survivors from this age when the subject was in the hands of a small group of botanists well known to one another. This applies to some of the conventions for the citation of botanical authorities and brief reference to publications in taxonomic treatments. In the formalization of botanical presentation, both descriptive and nomenclatural, all these leading botanists had set standards that were followed long into the future (Frodin, 1984).

Our group of notables had also orchestrated much of the labors of a farflung band of associates who strove to assist, in return for encouragement and approval. Among them had been Ferdinand von Mueller in Melbourne (Willis, 1949), William Harvey in Cape Town (Ducker, 1988), and Engelmann in St. Louis. All were productive in their own right, but also contributed importantly to joint works or resources available to Bentham, Hooker, or Gray. In the *Prodromus*, de Candolle had coordinated the work of 35 botanists in eight European countries (Stafleu, 1966). A comparable degree of wide cooperation on international projects is only now being rekindled and is made easier by such organizations as the International Association of Plant Taxonomists (Stafleu, 1988), as well as by modern technology.

EVOLUTION

Each of these botanists had taken up the new evolutionary thinking. Hooker, Gray, and de Candolle had used it as a basis for discussions of phytogeography and had been especially active in promoting its acceptance. Yet the system adopted in Bentham and Hooker's *Genera Plantarum* was modeled closely on that of the pre-Darwinian Augustin-Pyramus de Candolle. As Stevens (1984) has pointed out, the incorporation of the evolutionary time-axis and concepts of divergent evolution had remarkably little effect on the classifications they produced, which were often reminiscent of earlier ideas of a network of living organisms.

The Berlin School

The next major botanical phase was not a direct legacy from any of our four botanists. The focus shifted to Germany, where the German universities had been preeminent for some decades in research on plant structure, developmental morphology, and physiology, as well as providing training to many students from other countries including the United States. This continued with rigorous morphological interpretation, static in some aspects, but with valuable precision of analysis. Adolf Engler had been appointed in 1889 as professor and director of the botanical garden in Berlin. There, and previously at Breslau (now Wroclaw) and in his general approach, Engler followed in the steps of his mentor August Eichler, but with vastly expanded aims (Stapf, 1930). Engler's name "symbolizes the spectacular development of German botanical systematics in the late nineteenth and early twentieth century" (Stafleu, 1972), and his *Syllabus* (1892) has been followed by much advanced and very useful further editions up to recent times (Melchior, 1964). The *Pflanzenfamilien* (Engler & Prantl, 1887–1915) and *Pflanzenreich* (Engler, 1900–

1953) have been the last of the great encyclopedic treatments of the plant kingdom. These projects, envisioned by Engler and assisted by Prantl and many others, continued for decades on much the original plan. Only when the current project of Kubitzki and others (Bates et al., 1980) comes to fruition will their status be challenged.

Engler's attempt to arrange plant orders and families in what he conceived to be phylogenetically determined sequences was only partly successful since it did not recognize the extent of reduction trends that produced structurally similar forms.

Decline and Rise

Encyclopedic projects such as Engler's, however vast their scope and achievement, were assembling existing knowledge rather than moving ahead in scientific concepts or methodology. By now the rush of exotic discoveries had lost impact and the physical sciences and biochemistry were on the rise. In both botany and zoology, taxonomy was in decline before the end of the nineteenth century and was seen as a scientific backwater, unattractive to the best minds. Botanical taxonomy was continuing the task of cataloging and naming the world's plants, with more emphasis than before on the cryptogamic groups. Around the world the general rate at which herbaria were founded (Ma, 1988) was increasing almost exponentially, but this was not an indication of the scientific standing of herbaria.

Rollins (1965) expressed it well: near the end of last century "herbaria were respected centres of teaching and research. The most eminent men of botany were associated with them." By contrast, over some decades up to the middle of the present century, "Having established its place in the University and in the Museum, the herbarium attracted less venturesome scholars, who narrowed the dimension of their activities . . . the image became one that reflected stultification, diffidence and rigidity without sinews to bind it to the main stream of biological teaching and research."

Taxonomy would be revitalized a few decades later from a source that was already at hand early in the present century—the new field of genetics. Hull (1988) recounts how several workers around 1900 independently experimenting on character segregation came upon Gregor Mendel's publications. Soon genetics was a flourishing experimental and theoretical field, but at first genetics was seen to be incompatible with and opposed to Darwinian evolution. The reconciliation and fusion of genetics and evolution came when Fisher, Haldane, and Wright began to develop concepts of the structure and dynamics of populations, and Darlington (1937) expressed the relevance of genetics to plant evolution.

The integration of genetics with evolutionary biology at the taxon level came later with the "new systematics," which was led by zoologists Dobzhansky, Simpson, Mayr, and Huxley, but which affected all systematic biology.

New Data Sources or Panaceas?

The rediscovery of Mendel's work was followed by the identification of chromosomes as genetic material and the realization that chromosome morphology offered characters for study.

Moreover, karyology sometimes suggested hypotheses about processes and directions of evolutionary change, although these were often hedged with statements that certain directions were "unlikely" rather than "excluded from consideration." Early work was summarized in *Variation and Evolution in Plants* by Stebbins (1950), which helped to inspire a generation of research students of my time, as Darlington (1937, 1939) had done for our mentors in this field. Applications of karyology were numerous at all levels, from infraspecific to considerations of base numbers and major trends for orders and families and for the angiosperms themselves (Raven, 1975). The extent and patterns of chromosomal variation led students of phylogeny to mistrust or downgrade the importance of chromosomal information for broad considerations (Raven, 1975), but such information has thrown important light on relationships and processes in many groups (Moore, 1978).

Along with chromosomal studies in the early decades of this century went biosystematics. This field seems to have been variously defined, certainly embracing studies of variation, population structure, and breeding systems, but at other times taking in karyology, cytogenetics, and the whole of genic molecular evolution (Grant, 1984; Vickery, 1984). In line with biosystematic thinking, taxonomists for decades sought justification of their categories from biological species concepts. Ehrlich & Raven (1969), Raven (1977, 1980), and others have shown that much that has been claimed about species as interbreeding populations does not accord with the situation in nature. They pointed out how limited the gene flow is between the distant local populations of a widespread species, but that members of such a species are held together by common ecological constraints. It is scarcely an elegant solution that the term "species" is now

concurrently applied to various different concepts, but at least some consensus seems to have been reached in botany (e.g., Davis & Heywood, 1963; Raven, 1976, 1986; V. Grant, 1981; W. Grant, 1984; Haufler, 1989) so that semantics no longer dominates over observations on the situation in nature. In general, biosystematics, at least as narrowly defined, seems to have contributed less to taxonomy than to understanding evolutionary processes and part of its field has been claimed by its vigorous offspring, pollination ecology. It remains a useful approach in its own right but somewhat separate from the main thrust of taxonomy.

Alston & Turner (1963) characterized the first half of this century as the cytogenetical phase of systematic biology, whereas they designated 1950 onward as the biochemical phase. Twenty years later Harborne & Turner (1984) made a more modest claim, stating that they did "not believe that biochemistry represents a panacea for all systematic problems" and indeed that the role of systematics as a framework for the ordered arrangement of observations applies as well for biochemical data as for morphology. Secondary metabolites have proved their use, and compendiums such as Hegnauer's (1962–1973) have a wealth of data, especially for studies at higher taxonomic levels. Indeed, the strength of Dahlgren's system of the flowering plants (1980) lies mostly in placing greater emphasis on chemical characters than do other modern systems. So far, the chemical data have generally supplemented morphological data rather than replacing them. The first biochemical phase of taxonomy seems to have largely bypassed the majority of taxonomic practitioners until now. Remaining oblivious to the macromolecular phase will not be so easy.

In respect to systematics, both cytogenetics as envisaged early this century and chemosystematics failed to fulfill their early promises, but they have found their place as valuable aspects of multidisciplinary taxonomy. Perhaps one of the surprises has been the resurgence of morphology.

The basis of early classifications was exomorphology, but the range of relevant structural aspects has been greatly widened as means of observation improved and as concepts of homology have been more strictly applied. Thus that excellent symposium "The Bases of Angiosperm Phylogeny" (Walker et al., 1975) included structural topics ranging from floral or vegetative anatomy and morphology to palynology, embryology, and ultrastructure. The new findings have been especially rewarding at the upper taxonomic levels, as with structure of leaf teeth (Hickey & Wolf, 1975) or the ultrastructure of sieve-element plastids (Behnke, 1975).

A related advance has been the integration of critical morphology with cladistic and biogeographic approaches into botanical palentology (e.g., Crepet & Nixon, 1989). A better explored fossil record, with more precise morphological observation and comparison, is throwing more light on the interpretation of living groups (e.g., Dahlgren, 1983).

Emphasis on Analysis, Phenetic and Cladistic

Many biologists were well pleased to be working with these expanding fields of data but others looked to new possibilities of making systematics more objective through attention to the philosophy and practice of data analysis. The early converts to these numerical methods seemed to find their satisfaction more in methodology than in improving knowledge and classifications of organisms.

In retrospect, numerical phenetics based on exomorphology seems something of an aberration and its theoretical basis (or lack of it) was much criticized at the time (e.g., Mayr, 1965; Johnson, 1968, 1970). But it held centerstage in both zoological and botanical taxonomy during the 1960s into the 1970s, and the major expositions of this approach were much followed (Davis & Heywood, 1963; Sokal & Sneath, 1965; Sneath & Sokal, 1973).

Hull (1988: 130) gives graphic expression to the next turning point:

> "In the hubbub over numerical taxonomy, hardly anyone noticed scurrying around in the underbrush the ancestors of the next dominant group in systematics, as inconspicuous and active as the progenitors of the mammals had been in the age of the Dinosaurs."

Cladistics as an established approach dates from the "discovery" by Kiriakoff and others of the work of Willi Hennig (Hennig, 1950, 1966), although numerical methods to elucidate phylogenetic lineages based on synapomorphies were independently developed around that time or soon after by others (e.g., Wagner, 1961; Camin & Sokal, 1965; Johnson & Briggs, 1975). In his comprehensive account of the development of cladistics, Hull aptly describes Henning's contribution:

> "The methods he described for reconstructing phylogeny were not especially new. Rather his chief contribution was the clarity with which he set out his principles and the emphasis he placed on them."

Since then, cladistics has presented an exceptionally argumentative scene as it challenged the survivors of the "New Systematics"—great phylogenists like Mayr and Simpson. Cladistics has sharpened taxonomic thinking and brought emphasis back to the evolutionary basis of nature's hierarchical patterns (e.g., Eldredge & Cracraft, 1980; Wiley, 1981; Nelson & Platnick, 1981; Farris, 1983; and the greater part of the contents of *Systematic Zoology* for more than a decade). Even so, many cladists (pattern cladists) sought to make their analyses as theory-free as possible, to separate the analysis from any theoretical explanation that might be used to interpret it.

Guiding principles have been monophyly or holophyly, use of outgroups or hypothetical ancestors, and parsimony. Similarity in plesiomorphous features is dismissed as irrelevant, and grouping into clades depends on synapomorphies alone. Some practitioners seem to forget that evolution is not necessarily parsimonious but rather that the choice of the shortest tree, with fewest steps from the common ancestor to the member taxa, depends on a philosophical approach that excludes uncorroborated suppositions and unnecessary steps not decreed by the data. The evaluation of character homology has led to much desirable reinterpretation of the morphological and developmental equivalence of features. Methods differ in whether they accept trend reversals or work under a restricted parsimony model. Important concerns are falsifiability of hypotheses, and the writings of Karl Popper and other philosophers are much quoted.

Cladists have exaggerated the extent of innovation in their approach (Ghiselin, 1984) and have often been overconfident about their results. Misleading and ill-based conclusions can come from misinterpretation of homology, lack of commensurability or balance in the characters selected, extensive parallelism, or from methods that do not show the full extent of competing trees of equal or near-equal length. Such problems are now being addressed by more critical assessments, improved methods (e.g., PAUP, Swofford, 1985), and concentration on "robustness" with consensus trees and "bootstrap" or "jack knife" procedures.

Practical difficulties arise from paraphyly (Cronquist, 1987; Johnson, 1989) and bear consideration. When paraphyly is well corroborated it is often appropriate to accept a new classification based on cladistic analysis. But, for instance, should one fail to give taxonomic recognition to a well-marked group (one that is itself holophyletic) on the grounds that it leaves a paraphyletic residue that is not yet resolved? Perhaps classifications may include both monophyletic and paraphyletic groups, with those that are not monophyletic clearly identified as such (as suggested by Wiley, 1981).

Cladistics has been justified on the grounds that "truth emerges more readily from error than from confusion. Perhaps [Hennig's] phylogenetic systematics might prove to be mistaken, but no one was going to be able to accuse it of being confused" (Hull, 1988), and cladistics has been tagged "cladistics: being wrong **with confidence**" (Penny et al., 1990); these judgments carry a valid warning but not a reason to reject cladistics. It has proven its power, and almost any issue of a modern systematic journal will show it as the method of preference for intensive investigations of plant groups at all levels. Noncladistic similarity methods are, however, widely but not unanimously advocated for analyzing macromolecular sequence data, as mentioned below.

Cladistics also concentrated attention on another problem: if a genealogical tree has been established, how should the categories of the taxonomic hierarchy be assigned to its branches? Major categories tend to be claimed by the divergence of groups at the base of the tree, leaving minor categories to assign to the most diverse and prominent groups. Thus, in the system of Bremer (1985) the flowering plants form subclass Magnoliidae within the Chlorobionta, whereas the Anthocerotatae are a superclass. This has logic, concentrates awareness on important new understanding, and is probably the way of the future. There is, however, some loss in communication as well as some gain: people are interested in "grade" aspects of organisms and their adaptive syndromes, as well as in their genealogies. Terms like 'amphibians' and 'reptiles' have conveyed information on levels of organization, even if we now find that they refer to paraphyletic assemblages.

Macromolecular Biology

Cladistics swept through systematics as something of a revolution little more than ten years ago. Already a new turning point is at hand—the application of macromolecular genetics to systematics.

Isozymes, the first manifestation of this approach, made their appearance in taxonomy in the 1960s. Some early workers on isozymes have since led the charge into nucleic acid studies, but isozymes continue to have a place, especially in work at the lower taxonomic levels including investiga-

tions of population variation (Crawford, 1983; Giannasi & Crawford, 1986; Ferguson, 1988; Brown, 1990). Isozymes sample only nuclear genes that are expressed as enzymic or structural proteins (Clegg et al., 1984), and exclude genes from other organelles.

Next came amino-acid sequencing of proteins, which has been described (Giannasi & Crawford, 1986) as "an approach whose time has come and gone (with regard to *plant* phylogeny) during the past two decades." Such sequencing has contributed importantly to phylogenetics of flowering plants at higher taxonomic levels (e.g., Boulter, 1973; Martin & Dowd, 1990). But proteins show many parallel base substitutions and this gives rise to distortions in their use to interpret phylogeny (Boulter, 1980).

Present emphasis is on base-sequencing of genomes. Genomes offer a large number of potential characters for study (Ritland & Clegg, 1987). They also have advantages of universality exceeding any morphological characters and approached only by a few cytological features. Some gene systems have been so conservative that all living things from the level of bacteria include homologous genes (e.g., those coding for hemoglobins, Appleby et al., 1990). Other gene systems have been quite labile and show differences between allied species or between individuals within a population (Clegg et al., 1984; Jorgensen & Cluster, 1988). Noncoding regions may provide data complementary to those from protein-coding regions since they are subject to different functional constraints (Zurawski & Clegg, 1987; Clegg, 1989).

The technical difficulties in obtaining data are being overcome, so that information is available from chromosomal, mitochondrial, and chloroplast genomes. Chloroplast DNA analysis provides data with exceptionally low levels of homoplasy, relevant to the time frame of the evolution of significant groups of flowering plants, and that lead to robust trees. Mitochondrial DNA is more variable in structure and organization in plants than is chloroplast DNA, and recombinant types arise in hybrids, whereas chloroplasts are strictly maternally inherited in most flowering plant groups. Ribosomal RNA contains both highly conserved and variable regions and so is useful over a wide time range (Baverstock & Johnson, 1990).

A notable example of informative restriction site analysis of chloroplast DNA is in the Asteraceae. The distribution of a large inversion suggests that the initial dichotomy was the separation of subtribe Barnadesiinae (Mutisieae) from the rest of Asteraceae, including from the three other subtribes of the Mutisieae (Jansen & Palmer, 1987, 1988; Bremer, 1987; Palmer et al., 1988).

The pace has accelerated in the last few years with important data coming from Fabaceae (Doyle, 1987; Doyle et al., 1990), Onagraceae (Gottlieb, 1988; Sytsma & Smith, 1988), Poaceae (Hamby & Zimmer, 1988), and various groups (Palmer, 1987; Palmer et al., 1988) including Caryophyllales, Orchidaceae, Solanaceae, Fabaceae, and studies within the genus *Brassica*.

The living collections of botanical gardens are coming into their own as accessible research material for macromolecular work, but the technology can now use minute amounts of nucleic acids so that herbarium specimens can serve as sources for enzymes for electrophoresis (Ranker & Werth, 1986) or for DNA (Doyle & Dickson, 1987), and even the partially degraded material of some fossils can give information (Paabo, 1989).

The data are voluminous even when only a few gene systems are investigated. If methods of numerical analysis were not already accepted procedures in systematics, they would have had to be invented now to cope with this flood of new data. The power and relevance of the macromolecular data are clear, but warnings against excessive confidence have been sounded. Penny et al. (1987, 1990) draw attention to problems arising when data are insufficient, not representative of the genome as a whole, or when methods of analysis lead to convergence on an incorrect tree (including cases where a tree is not an appropriate model).

Studies of chloroplast or mitochondrial DNA are elucidating the phylogeny of organelles, not directly that of the organisms that contain them. Thus the gene phylogeny may depart from the species phylogeny. For instance, maternal inheritance of mitochondria in higher animals (Neigel & Avise, 1986) produces anomalous results in comparisons of conspecific individuals and recently diverged species. As a result, the phylogenetic distribution of mtDNA may not be concordant with species boundaries. As mentioned above, chloroplasts are also strictly maternally inherited in most flowering plant groups.

Methods of analyzing molecular data have rightly generated much discussion. A two-step procedure with cladistic methods to produce trees and maximum-likelihood similarity methods to evaluate those trees (Templeton, 1983) appears to have advantages. Farris (1985) and Cracraft (1989) have called for cladistic methods to be used more generally with sequence data, but others have pointed to problems that may arise in parsimony analyses (e.g., Felsenstein, 1978; Jansen & Palmer, 1988).

Major Groups and Their Relationships

Cladistic studies within orders or large families have tended to show few synapomorphies marking the lower internodes of early-divergent clades, so that some or all of the major groupings are not robust (e.g., Myrtales and Myrtaceae—Johnson & Briggs, 1984; Rosaceae—Kalkman, 1988; Caesalpinioideae, the basal group within the legumes [lack of robust groups is clear from descriptive comment—Polhill & Vidal, 1981—rather than from formal cladistic analysis]). The hypotheses represented by competing trees in such analyses have nevertheless led to marked improvements on earlier views of relationships. Even more improvement toward robust phylogenies can be expected where such analysis has available macromolecular markers relevant to subfamilial or tribal groupings. Examples are in Asteraceae (Bremer, 1987, incorporating data from Jansen & Palmer, 1987) and in Faboideae (Doyle, 1987).

Systematics this century has worked through a range of phases, enlarging the spectrum of new approaches and scarcely ever relegating any as irrelevant. As a result, a valuable development has been the symposium that brings many approaches to focus on a particular large group, usually a family or an order. Apiaceae (Heywood, 1971), Asteraceae (Heywood et al., 1977), Solanaceae (Hawkes et al., 1979), Fabaceae (Polhill & Raven, 1981; Stirton, 1987), Myrtales (Raven, 1984), Poaceae (Soderstrom et al., 1987), Hamamelidae (Crane & Blackmore, 1989), and others have benefited from this treatment. Often considerable consensus has emerged but sometimes such a meeting of minds has emphasized the divergence of views, as with the status and circumscription of genera of Asteraceae (Lane & Turner, 1985).

Still wider synthesis has been the task of those who have developed systems of classification for the flowering plants as a whole. Impressive arrays of features contributed to the systems of Thorne (1981), Cronquist (1981), Dahlgren (1980; Dahlgren et al., 1985; Dahlgren & Bremer, 1985), and Takhtajan (1987). The next round of systems will differ from these by extensive use of macromolecular data.

Work has not been concentrated on the flowering plants alone. The algae have been recognized as a heterogeneous assemblage of groups. Fungi and bacteria have been more adequately divorced from green plants, and such discordant concepts as the broadly conceived pteridophytes and the gymnosperms are tending to drop from scientific usage. Homologies between major groups have been investigated and, with the increased range of morphological data available, have been the subject of cladistic studies (e.g., Bremer, 1985). The symbiotic origin of the eukaryotic cell has been a major unifying theory, now happily confirmed by the genic homology of mitochondria with "purple bacteria" and of chloroplasts with cyanobacteria (Pace et al., 1986). The higher taxonomic levels especially can be expected to repay macromolecular studies if suitably conservative genes are chosen.

Floras, Tensions and Synthesis

This review has looked briefly at the outstanding trends over a century. But what were the taxonomists actually doing? Fortunately they were mostly not poised waiting to catch each new bandwagon as it came along. Mostly they were describing taxa, writing floras and monographs, developing the resources of collections and published work that we now have. Usually they applied only a sample of the range of available approaches to the classification of each particular plant group.

Thirty years ago Stafleu (1959) characterized the state of plant taxonomy as an "age of floras and floristic work," noting that this was partly at the expense of synthetic and monographic studies. This characterization applies with greater force today. The increasing recognition of threats to the diversity of the biota, and also recognition of the value of that diversity, have helped taxonomists to obtain funding for large flora projects, regional, national, and international. Floras of the U.S.S.R. and Europe have been completed. Projects for Australia, China, India, North America, and South Africa have joined such longer-established works as *Flora Malesiana, Flora Neotropica, Flora of Tropical East Africa* (references in Frodin, 1984), and compilations such as Med-Checklist (Greuter et al., 1984–1989) in providing accessible information on the world's flowering plants.

Frodin (1984) observed that so little change in style has taken place in floras over 140 years—since Torrey, Gray, Bentham, and Hooker—that "One who compares some current American state floras with Torrey's *Flora of the State of New York* might be forgiven for thinking that the modern works had been written by descendants of Rip van Winkle"—and North America is not the only continent to which such comment applies.

Plant taxonomists are used to living in a scientific culture of some tension. Bibliographic search back more than 200 years and Latin diagnoses are still part of their stock-in-trade, although moves to change the former are being considered. Yet for

50 years intensive studies using varied techniques have competed with descriptive flora and monographic projects. Macromolecular genetics now offers involvement with aspects of one of science's fastest-moving fields. There are serious choices to be made in how much of their resources institutions and individuals should devote to their different responsibilities for flora projects, revisions, and using the most powerful tools yet available to elucidate phylogenies and thus improve classifications.

A challenge at present is to maintain cohesion in systematics across these streams so that the new developments are a scientific stimulus to the subject as a whole. Academic teachers of biology must have a broad appreciation of these approaches in research and education if the training they provide is to be relevant to the eventual careers of most research students in systematic and evolutionary biology. On the other hand, the herbaria and other institutions, while carrying the major part of most floristic projects, will need to respond positively to new developments if these organizations are to remain central to the mainstream of scientific taxonomy.

With environmental destruction and change now rampant, it was the taxonomists of these last hundred years that sampled the world's biota at the richest development it has offered for study. The immediate future gives the best chance humanity will have to investigate the diverse products and processes of evolution.

The concise flora has been an appropriate reaction to the need to record plants in regions under threat and to obtain information on diversity to support the case for conservation. This view has recently been strongly supported by Nooteboom (1988) and by Bramwell (1989). Equally, however, most macromolecular studies require access to live plants. The living collections of botanical gardens are becoming more important as research materials, just as the herbarium collections built up over the last century have become increasingly irreplaceable (Raven, 1988).

Macromolecular studies of different gene systems have commonly, but not always, given consistent results. There is particular need to investigate cases where there is disparity between results from DNA and from morphological data (Sytsma & Smith, 1988). There are instances of isozymic information on allied species corroborating morphological similarities but giving results quite at variance with comparisons of chloroplast DNA in ferns (Yatskievych & Moran, 1989) and with mitochondrial DNA in fishes (Dowling & Brown, 1989). Studies on *Lisianthus* (Gentianaceae) have given similarly discordant results (Sytsma & Schaal, 1985). It may be relevant that these apparent "failures" of DNA analysis are all applications to groups of closely allied species, whereas there has been greater success at higher taxonomic levels. As information accumulates, it may be possible to select methods appropriately to particular levels and also to interpret such discrepant findings.

Patterson (1987) postulates that "molecular homologies are no more secure, and are possibly more precarious than morphological ones," and McKenna (1987) writes, "It should also be obvious that molecular studies can suffer from exactly the same ills that beset comparative anatomical ones: a touchstone has not been found." Indeed, the succession of failed panaceas in systematics should be heeded as a warning. Nevertheless, by seeking congruence of data from different gene systems and from morphology, it appears that macromolecular methods will often produce convincing phylogenies at many taxonomic levels, and they offer a vastly expanded sample of characters.

"Reliable" taxonomies have long been contrasted with speculative phylogenies, even though the assignment of levels in taxonomic hierarchies has been accepted as partly a matter of subjective judgment. The situation is tending to be reversed.

Patterson (1987) observed that as little as 30 years ago, when phenetics was at its height, it was thought that "classification by genealogy might be a laudable goal, but not one that was attainable." In *The Origin of Species*, Darwin (1859: 486) had predicted that "Our classifications will come to be, as far as they can be so made, genealogies." To the extent that the promise of macromolecular systematics is realized, phylogenies inferred from sequence data and considered in the light of morphological and other data sources may become frameworks to use in asking important questions in other areas of biology.

If phylogenies can be accurately and reliably de ermined at many taxonomic levels from macromolecular information, Gottlieb (1988) is right to claim that this offers dramatic new opportunities to systematists. Human interest in organisms is not limited to their relationships, but is also in how they work as functional, adaptive systems and how genic change has been expressed in ontogeny and in phenotypes. Botanical systematics will still be an unending and widening synthesis—but on new terms.

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A HISTORY OF BOTANICAL NOMENCLATURE[1]

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ABSTRACT

I divide botanical nomenclature into three partly overlapping periods: the schismatic period (1840–1930), the dark ages (1915–1950), and the IAPT renaissance (1950–date). The schisms began with the 1843 British Association for the Advancement of Science approval of zoological rules and became manifest with the 1867 Paris Congress approval of Alphonse de Candolle's botanical "laws." Reunification efforts, such as those by Dall (1877.12), failed. The contemporary rise of "Darwinism" added to the divisiveness. By the late 1800s, various botanical centers had or were evolving modified or different Codes from the Candollean, not to mention fully formed Codes from "outsiders" like Saint-Lager (1880.03?, 1881.04) and Kuntze (1891.10). The 1905 Vienna Congress eliminated all but the Brittonian (American) schism, which continued until the 1930 Cambridge Congress compromises. A nomenclatural "dark age" descended when the 1915 London Congress was cancelled because of a subsequent engagement, World War I. The next congress (Ithaca, 1926) declared itself incompetent due to insufficient international representation. The 1930 Cambridge Congress revised the 1912 Brussels Code but, largely because of the death of Briquet in 1931, its Code appeared only a few months before the 1935 Amsterdam Congress that amended it. Again a World War struck and no official Amsterdam Code was ever produced. The 1950 Stockholm Congress saw the establishment of the International Association for Plant Taxonomy, its journal, *Taxon*, in which all Code amendment proposals now appear, and its serial publication, *Regnum Vegetabile*, in which all subsequent Codes appear at the remorseless six-year pace of the congresses.

The Linnaean aphorisms (1737.07) concerning nomenclature basically concern generic nomenclature (the first part of the binary system of nomenclature). Few seem to have realized that the species names Linnaeus discussed are the diagnostic phrase names, not the species epithets, called nomina trivialia, that Linnaeus later, for plants (1753.05.01), adopted in his revolutionary binomial (or biverbal) system.

The Linnaean nomenclature (binomial) system has two facets: divorcing the name from the diagnosis and minimizing classification. Systems that totally eliminate classification, such as uninomial systems, are unwieldy. Systems that try to diagnose, such as phrase names, are unstable. Bergeret devised the worst of all possible systems, called phytonomatotechnie, a 15-letter uninomial system with each letter expressing a descriptive characteristic, such as *leglyabiajisbey* for *Belladonna*. Du Petit Thouars added a bit of the family name to each generic name (such as *Habenorchis* to replace *Habenaria*). Fossil nomenclature is still troubled by mixing generic nomenclature with morphology.

Priority had no part of the early schemes of nomenclature. Their authors, including Linnaeus, were focused on replacing the past. Linnaeus was the winner of this competition but contemporary and subsequent workers continued to devise new nomenclatural schemes and rules to overturn the past.

EARLY RECOGNITION OF MODIFIED PRIORITY (1813)

Augustin Pyramus de Candolle (1813), about to initiate the great *Prodromus*, gave a nice discussion of nomenclature of what might be termed good practices with examples. He (p. 250) favored priority except in the following five cases: (1) if the name was false and contradicted the characters of the plant, such as *Lunaria annua* (a biennial); (2) if the name was contrary to Linnaean practices such as pre-Linnaean or common names or if named by travelers who were not naturalists; (3) if the name was a later homonym of a name already published, be it in the plant or animal kingdom; (4) if the name was a later homonym or a tautonym created in the process of maintaining the epithet of an early name; (5) if the name was a nomen nudum, lacking at least a phrase sufficient to make recognition possible, such as "in a simple catalogue of a garden." De Candolle did not use such modern words as epithet, homonym, tautonym, or nomen nudum but that is what he talked about. This was

[1] I thank Krister Karttunen (Helsinki) and Ronald Stuckey (Columbus, Ohio), who shared their bibliographies on nomenclature. I also thank Werner Greuter, director, and the staff (Berlin) for access to and all facilities at their quickly regrowing library.

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still a biological code, revealed by the avoidance of homonymy with earlier names in zoology.

There undoubtedly are earlier authors who had the idea of trying to maintain usage, unlike reformers such as Linnaeus. The general idea was to maintain usage from Linnaeus by the principle of priority with certain modifications. It is the modifications that have caused most of the disagreements.

Beginning of the Break With Zoology (1843)

The approval of Strickland's 1843 Code by a committee of the British Association for the Advancement of Science officially began what I call a split. However, they were not thinking in terms of a split, as is clear from the second of the following quotations:

The first quote concerns the evil that they wish to address. "It consists in this, that when naturalists *are* agreed as the characters and limits of an individual group or species, they still disagree in the appellations by which they distinguish it." Further on they discuss the sins that create this evil.

Finally, so all will know how botanical nomenclature was perceived by zoologists (including Charles Darwin, a member of the Strickland Committee): ". . . we conceive that the botanical nomenclature of the present day stands in much less need of distinct enactment than the zoological. The admirable rules laid down by Linnaeus, Smith, Decandolle, and other botanists . . ., have always exercised a beneficial influence over their disciples. Hence the language of botany has attained a more perfect and stable condition than zoology and . . . its present backward and abnormal state. . . ."

One of the subsequently liveliest issues was the question of author citation in new combinations. This work recommended (for the first time?) citing only the author first publishing a name for the species (optionally in parentheses), irrespective in what genus the epithet was now used. Peter F. Stevens has suggested (in litt.) "that the development of this convention is associated with changes in the philosophy that species are created, fixed and immutable, and placed in similar genera; what came to be important in priority was who first discovered the unknown species, not who finally put it in the 'right' genus."

Candollean Laws of 1867

On 1 August 1867 Alphonse de Candolle finished the cornerstone work of botanical nomenclature for the meeting of the International Botanical Congress of 16 August 1867 in Paris. This 60-page paper has 11 pages of introduction, 19 pages of "laws" in 68 articles, and 28 pages of commentary. The commentary is particularly valuable because it comments on past usage with examples. One of the main issues (one-third of the commentary) concerns author citation, favoring the old way (only the name of the transferring author) but noting that others had introduced the new way (only the name of the author first publishing the basionym) in botany. The issue is exemplified by how to cite Robert Brown's *Matthiola tristis*, previously known as Linnaeus's *Cheiranthus tristis*; the old way is *Matthiola tristis* R. Br., and the new way is *Matthiola tristis* L.

According to Bentham (1878.12), it was the nomenclatural objections to J. Müller's treatment of Euphorbiaceae in the *Prodromus* that occasioned de Candolle's producing his *Lois*. See Seemann (1866.12.01), Gray (1867.01), and A. L. de Candolle (1867.05.01) for contemporary discussion. De Candolle indicated that Karl Koch's proposals (1866) to the London International Horticultural Exhibition and Botanical Congress provided the inspiration. Alphonse de Candolle was president of the London 1866 Congress and might have been stimulated to start thinking about codifying rules. However, I found little in Koch's proposals or the proceedings that would have been as inspiring as the nomenclatural novelties that Jean Müller slipped into de Candolle's *Prodromus*. Müller's major sin was to credit names, such as *Croton*, to himself when he redefined the taxon.

Apparently between 1 and 16 August 1867, a commission, composed of Du Mortier, Weddell, Cosson, J.-E. Planchon, Eichler, Bureau, and de Candolle (representing France, England, Germany, Belgium, and Switzerland), went over the proposed articles and suggested modifications in the form of motions to the Congress. At the Congress (cf. de Candolle, 1867.11) there were the first discussions of vital questions such as Order vs. Family, Cohort as a rank between Class and Order, long discussions about how to name hybrids, more debate on author citation for new combinations, even a mention of types in discussions. Otto Kuntze, who later will make himself famous in nomenclature, made a proposal about pleonasms and it passed. Eichler argued for replacing -ae- with -i-, as in *hederaefolia*, but was finessed by Alphonse de Candolle who said this was a matter of latinity and grammar, not nomenclature.

It is worth noting that the Code (1867.09.12) was not enforced like the current Code(s). It was "adopted by the assembly as the best guide to follow

for botanical nomenclature" (A. L. de Candolle, 1867.11: 208).

Within 18 months de Candolle (1869.06) felt compelled to address the questions and criticisms raised by "his" Code, including approbation. He gently demanded permission not to speak of the vexing question of author citation, pointing out that he seemed to have involuntarily provoked a kind of polemic and antipathy that rarely contributes to progress in science. He continued to avoid discussion of Greek and Latin because it doesn't involve nomenclature. I mention most of the issues that he addressed in his quiet and civil fashion (with my summary): (1) retroactivity of laws (pro); (2) saving the name when a taxon is subdivided (pro); (3) effective publication; (4) citation of unpublished names (ex favored over in); (5) names contrary to fact (con); (6) hybrids and cultivated plants.

Dall (1877.12) released an important survey of American zoologists with another Code, including the Candollean laws, for botanists and zoologists. This was not a unified (biological) Code because, when there were real differences (as the different endings for family names) then there were separate but contiguous articles. Otherwise an article pertained to both botany and zoology. For those interested, an excellent discussion of the differences between the two Codes was published in 1944 (see bibliography).

Saint-Lager was peeved by the Candollean efforts to maintain status quo, characterized as "continuation of disorder and anarchy." In 1880 he released his reform, aiming to overhaul all the "bad" spelling. This substantial treatment (155 pages, supplemented by 50 more pages the following year) covered most orthography questions (some that continue to vex us), applying pure classicism or peculiar conventions to change an astounding number of names or epithets. His ideas included (1) replacing *Panax* (p. 109) with *Panaxus* (at least we wouldn't argue about its gender) and (2) replacing genitive (p. 118) substantives (*nemorum*, *segetum*, *sepium*) with corresponding adjectives (*nemoralis*, *segetalis*, *sepicola*). The major effect was to make botanists aware that correctness could overturn usage and to strengthen support for the Candollean laws.

In 1883 Alphonse de Candolle published his "New remarks" (commented on by Asa Gray, 1883.12). De Candolle reviewed what happened over the past 16 years. His introduction commented on the Codes and Reports of nonbotanical groups. The opening part surveyed ongoing discussions article by article. The second part dealt with new matters, such as nomenclature of organs and fossils. The third part (61–76) included the 1867 Code with an indication of the changes proposed.

Kew Rule

The first mention of what will be known as the "Kew Rule" was by Henry Trimen (1877.06). This was objected to by de Candolle (1877.08). Hiern (1878.03) stoutly defended it. The first formal definition was by Trimen (1878.06: 171). Bentham (1878.12) protested ". . . creating a new name in order to combine an old specific with a new generic one." Jackson (1887.03) discussed his problems with what was to become *Index Kewensis*. The Kew Rule: "Our practice is to take the name under which any given plant is first placed in its true genus as the name to be kept up, even though the author of it may have ignored the proper rule of retaining the specific name [epithet], when transferring it from its old genus to the new." The Kew Rule was opposed again by Alphonse de Candolle (1888.10), but supporters perceived it as applying the principle of priority by maintaining the oldest applicable (binomial) name.

In January 1888 Asa Gray, the monarch of American botany, died, having supported the Kew Rule in one of his last papers (1887.12). Within months Nathaniel Lord Britton (Joseph Ewan assured me that the accent is on "Lord") began to show the first inklings of a drastic "new" nomenclature, shocking the Old Guard. The Candollean Code was under attack and promised to flood the new Index with unnecessary names. Many new combinations appeared in Poggenberg et al.'s (1888.04) *Preliminary Catalogue*, hailed by Greene (1888.06) as the "opening of a new era," but attacked by James Britten (1888.09) and Alphonse de Candolle (1888.10) as "mischievous," despite a spirited defense by Britton (1888.10).

Kuntze Strikes (1891)

Late October 1891, Kuntze's new *Revisio* with 1,074 replacement genera and 30,000 new combinations appeared, a nomenclatural schism of the first order. Kuntze had a very broad view of what constituted homonymy, treated 1737 as the starting point, and that claimed he was only actually applying the Candollean Code.

Kuntze's work is, like Saint-Lager's, essentially forgotten, but is full of examples and repays study. It is worth trying to realize what an impact his work had at that point. Geneva (Alphonse de Candolle) discontinued the great *Prodromus* in 1874,

Kew (Bentham and Hooker) finished the *Genera Plantarum* in 1883 and (Jackson) had just sent *Index Kewensis* to press, Berlin (Engler) began *Die natürlichen Pflanzenfamilien* in 1888. Suddenly thousands of names were thrown into question, most perhaps challengeable (say by locking on 1753 rather than 1737) but many were not.

The major attack came from German botanists. In April 1892 the German Botanical Society appointed a committee to prepare a supplement to the *Lois* of four propositions (theses). This was mailed to 706 botanists, requesting support and comments on each proposal (called "pamphleteering" by Weatherby in 1949.01). The four were: (1) priority of generic names from 1752; (2) rejection of nomina nuda and seminuda, including generic names based on simple figures and exsiccata without description; (3) retention of generic names differing only by the last syllable or inflection, even if they differ only by one letter; and (4) conservation of listed generic names.

The results of this poll, with comments received, appeared in Paul Ascherson's report to the Society (1892.07) and again at the September Botanical Congress in Genoa (400th anniversary of Columbus). Dall (1877.12) also had used a poll but was more interested in principles than in what to my eye appears to be "damage control." Also included was the first published list of generic names to be conserved, another effort to maintain usage threatened by Kuntze who (1895.11, if not before) termed the list an "Index inhonestans."

There was what in retrospect can be seen as a passing of baton by the nomenclatural leader. Briquet, who had included nomenclatural observations in his 1891 treatment of mints for Burnat's *Flore des Alpes Maritimes*, published (1892.02.04) his comments on what Kuntze had done to the mints. Briquet's evidence was cited by Alphonse de Candolle (1892.05) in one of his last nomenclatural papers before his death (1893.04.04).

Rochester Resolution of 1892

In the meantime a botanical club (with N. L. Britton) held a meeting within the American Association for the Advancement of Science (A.A.A.S.) in Rochester, New York, in August 1892. Their proceedings (Fairchild, 1892.09) included the Rochester Resolutions (later called the Rochester Code), which accepted the Paris Code of 1867 with eight exceptions: (1) priority was fundamental; (2) starting point was 1753 for genera and species; (3) the original specific name [epithet] was to be retained unless a tautonym or later homonym; (4) no later homonyms; (5) publication of generic names either by distribution of printed description or by citation of one or more species as examples or types, with or without diagnosis; (6) publication of species names either by printed description or with reference to previously published species as a type; (7) later similar generic names are not to be rejected on account of slight differences, except in spelling; (8) in case of transfer of a species to another genus, the original author must be cited in parentheses, followed by the author of the new binomial. They also approved sending Lucien Underwood to the Genoa Congress to deliver their resolution.

The September 1892 Botanical Congress in Genoa was obviously the place where a rousing battle could be expected.

Underwood (1892.11) reported on the polyglot sessions. Ascherson presented the substance of his recently published report concerning Kuntze with four proposals. The Rochester platform was presented. After the discussion the first three Berlin propositions were approved with 1753 (a Rochester resolution) for both genera and species. All else (conserved names and the Rochester resolution) was referred to a committee (Penzig 1893.04?: 439), which was to report to the next International Congress (Paris, 1900).

Madison Rules of Unmodified Priority (1893)

In August 1893 a group of American botanists, meeting at Madison, Wisconsin, decided to amend what now are now being called the "rules of nomenclature" adopted at Rochester (1892) and voted to change "Section III" of the Rochester Code by striking out all after the word "retained." This meant that a species epithet must be retained (restored) even if it involved a tautonym or a later homony. They also approved "that precedence in the same volume be regarded as priority," a modification of the first section. Although the Rochester/Madison resolution (1893.09) did not mention types, the idea of page (and place on the page) priority, i.e., first listed species or specimen, was used for typification by practitioners of the new school until the (1907.04) Brittonian (American) Code provided ways around the first "listed." Indeed, the major point of these rules, aside from astounding brevity, clarity, consistency, and positiveness, was that they admitted no exceptions. If you found the earliest name, your troubles were over for all time. Also, practitioners had the moral

high ground in that you recognized the earliest proposer and nothing could be fairer.

Note that what Saint-Lager, Kuntze, Britton, and others (as radicals) emphasized are the rules themselves, never mind upsetting usage, which was only a short-term consequence (cost). The Candollean (conservative) concept was to try to maintain the status quo, never mind some complexity of rules, which are really of no importance. Both concepts would agree that stability is the goal of nomenclature, but one wonders if the interaction of these two schools doesn't result in a Code with the worst of both worlds: a complex and constantly changing Code (trying to maintain past usage) and constant conservations (to set aside rules that, despite complexity, are not maintaining the past).

Kuntze Strikes Back

In July 1893 Kuntze published a second dose (first part of the third volume) of his *Revisio*. It had two features, a detailed comment on each publication (> 50!) that commented on his first dose and his *Codex Nomenclature Botanicae Emendatus* in German, French, and English in three columns with parallel text. Nothing was too fine to escape his caustic and withering comments, including the Rochester Resolutions, which were far closer to him than any other.

John Isaac Briquet, who was to dominate nomenclature for more than 30 years (like Alphonse de Candolle), readdressed (1894.02) the imbroglio with a discussion of eight questions and a conclusion involving Kuntze's impact on the generic names of Labiatae. This work was important for the comments on, among other things, nomina nuda and seminuda [subnuda], Patrick Browne, Rumphius, recycling names fallen into synonymy, still-born names, the role of pre-Linnaean documents, and infraspecific nomenclature. He also proposed 10 modifications of the *Lois*.

Kuntze (1894.07) discussed several recent attacks, expounding on Thouar's orchid names and other positions of Pfitzer, page priority (against the Madison amendments), an obligatory register for plant names, "once a synonym always a synonym," and so on.

By 1895 Ascherson and Engler were all that were left of the 30-member international commission recognized at the 1892 Genoa Congress. They put forward six propositions (1895.01), of which the last two involved avoiding names that have not been used for 50 years, which would become an element of the Berlin Rules.

Americans were showing an increasing disarray concerning their Code(s); the Harvard Code appeared on June and August 1895 with five conservative points. The latter (Anderson et al., 1895.08) was signed by 74 American botanists "of various degrees of repute," a comment made earlier about the signers of the Rochester/Madison resolutions.

Berlin Rules (1897, 1902)

Engler and his staff signed 14 rules for the Berlin Garden and Museum that appeared in June 1897. This was translated immediately into English (1897.08) and French (1897.09), often with comments. The Rules: (1) Priority was usually to be maintained (species from 1753, genera from 1754). (2) Generic names could be dropped if not in general use for 50 years from establishment unless restored because of the 1867 *Lois*. (3) Series were to end in -ales, families in -aceae, with exceptions for Coniferae, Cruciferae, etc. (4) For gender one must follow classical designations or, for later names, usage in *Nat. Pflanzenfam*. Changes ought not be made except for notorious errors in designations from proper names. (5) Generic synonyms were not to be applied in an altered sense for new genera or even sections. (6) Priority was to rule in species names unless objections were raised by monographers. (7) Parenthetic citation of authors was to be used for new combinations, unless the author himself placed the species in another genus. (8) Linnaean capitalization of species names was to be used (for epithets derived from personal names or names of former genera). (9) Rules were given for forming generic names from personal names. (10) One must change -ae- to -i-, as *menthifolia*, not *menthaefolia*. (11) One must avoid tautonymy (incl. *Elvasia elvasioides*) and depart from priority in case of gross geographic errors (North American *Asclepias syriaca* L.). (12) Hybrids must appear as a formula of both parents (in alphabetic order) with multiplication sign between (binomial nomenclature unsuitable). (13) Manuscript names, horticultural names, designations in trade catalogs had no rights; a printed diagnosis was required. (14) No changes permitted to a generic or specific name unless moved by weighty reasons such as Rule 11.

A supplement to the Berlin Nomenklatur-Regeln was published by Engler et al. (1902.08.29).

Kuntze Strikes Again

In September 1898 Kuntze released the last two parts of the third volume of his *Revisio*. One sig-

nificant document included is a *Supplement* to his *Codex Nomenclaturae Botanicae Emendatus.*

Paris Congress of 1900 (styled the 1st International Botanical Congress)

By October 1900 the stage was set for fireworks but the Congress unanimously decided to put someone in charge (John Briquet) and revise the Code at the next Congress. This was the beginning of the office of rapporteur général. Hua (in Perrot, 1900: 475–486) made a detailed proposal to establish an international periodical for publication of new names, a forerunner of a proposal referred to a subcommittee for registration of publications.

Kuntze struck again, this time (1903.12) with Thomas Erik von Post in the *Lexicon Generum Phanerogamarum*, including his *Codex Brevis Maturus*. The work applied Kuntze's Code to phanerogam generic names, had a bunch of cryptogam generic names and, in the second part, dealt with names above generic rank, all warranting a look by those interested in such.

Kuntze was given little recognition. Stafleu (in *TL-2* under Post) excerpted Barnhart's (1904.04) comment about Kuntze, "Possibly the vituperation poured upon all who disagree with him has prevented his ideas from receiving as serious consideration as they deserve. It is certainly unfortunate that he should regard himself as an infallible referee upon all points in dispute and hurl anathemas at all who refuse to acknowledge his authority, characterizing their propositions as 'dishonest,' 'inexecutable,' 'false' and 'lawless.'"

Brittonian (American) Code (1907) and Its Precursor (1904)

The Americans were divided and criticisms were being published, such as that by Fernald (1901.11), pointing out instability (actually inconsistencies) of practitioners of the Rochester resolutions. In early 1903 the Botanical Club of the American Association for the Advancement of Science appointed a Nomenclature Commission. They produced a "Code of Botanical Nomenclature" (1904.05) with four principles, 19 canons, and separate sections on orthography and citations. This came with a simple proposal to the Vienna Congress, "the laws of 1867 be amended by abandonment of all its articles and substitution of the appended Code." This proposal failed at Vienna in 1905, leading to the Philadelphia "American Code of Botanical Nomenclature" of 1907.04, which should be called Brittonian rather than American. The basic text was mostly unchanged from the originally proposed Code (1904.05), but there were changes in Canon 15 (application of generic names) as well as inconspicuous additions elsewhere. I mention three definitions of now obscure terms (metonym, typonym, hyponym, respectively taxonomic synonym, nomenclatural synonym, and name of an unidentifiable taxon).

Weatherby (in Sherff, 1949.01) pointed out that this Code had at least one large crack compared to the ancestral Rochester/Madison resolutions' iron-clad insistence on priority: it gave an elaborate series of directions for choosing types other than the previous implicit recognition of the first listed. Apparently the practitioners of the Rochester/Madison resolutions were upsetting more usage than they felt necessary and were willing to compromise their simple and brief Code with exceptions that took up more space than the original resolutions in toto.

Vienna Congress of 1905 (2nd Congress, 1st Code)

Briquet tracked down all reasonably explicit proposals since 1867 to change the code, translated them into French, and devised an organization. Thirty-eight publications were accepted as having specific proposals. This is a remarkable document, a key to the past. After all was compiled and organized (Nov. 1904), he sent it to the 39 members of the commission with his comments as rapporteur. They were to vote and return all by 20 January 1905 (31 did). Briquet (1905.03.15) laid out all in four columns: (1) original (1867) text, (2) proposed change(s), (3) the rapporteur's observations to the Commission, and (4) text recommended by the Commission.

The Congress convened in June 1905 in Vienna, capital of the flourishing Austro-Hungarian empire. This was the first meeting devoted solely to the vexing "problem of nomenclature." They had an immense amount of business with potential to end or descend deeper into chaos. It is fascinating to read how the proceedings were laid out (order of business), who had votes, and who did what. For example, N. L. Britton nominated Wettstein for president of the Bureau and proposed that French be the official language of nomenclature. Both were approved. Those wanting to speak had to submit a slip with their name and position (nom et qualité) to the president. Speakers were given five minutes (ten by exception) and only could speak twice on

the same subject. In fact, this Congress provided the model still followed by our nomenclature sessions.

The proceedings (Briquet, 1906) were also well spelled out, with a concordance of the 1867 *Lois* with the Rules and Recommendations of the 1905 Congress, the Code (principally for vascular plants) in French, English, and German with the now conserved generic names.

Among the many accomplishments of the Vienna Congress were the establishment of the first imposed international Code (the 1867 *Lois* was only recommended as the best guide to follow). It did not satisfy Kuntze, but he died in early 1907. The Brittonian Americans, although they had won some victories, were not happy that names still were not applied according to types and were allergic to the new requirement that Latin had to be used for publishing names of new taxa, considered arbitrary. The Americans, at least those supporting N. L. Britton, therefore settled more firmly into the Brittonian (American) Code, a rupture that would continue for twenty-five years.

The Brussels Congress of 1910 (3rd Congress, 2nd Code)

Aside from the nomenclature section, there was also an important section on bibliography and documentation. The paleontologists, phycologists, and mycologists made many proposals. Harms's proposals on conserving fern names passed. Briquet tendered his resignation but, when everyone was upset, got what he really wanted, help. Harms was elected vice-rapporteur, the beginning of that office.

The 1915 London Congress was never held, because of the outbreak of World War I in 1914.

Two people were particularly important in the years soon after World War I: Albert Spear Hitchcock (US) and Thomas Archibald Sprague (K). Each published initiatives that would ultimately mesh. In April 1919 Hitchcock presented some rules for fixing types of generic names that would (1921.04) become the "type-basis" Code. Did you realize that conservation of generic names, passed at the 1905 Vienna Congress, still did not involve listed types?

Sprague's initiative was to publish (1921.06) a thoughtful paper on plant nomenclature titled "Some suggestions." This appeared in the *Journal of Botany* with the editor's (James Britten) invitation for comments. The paper stimulated a series of pleasant and unpolemic contributions from (mostly) Americans and British botanists that strongly signaled compromise and recognition that unity in nomenclature was better than ongoing strife.

In July 1924, Alfred Barton Rendle presided over a discussion at the Imperial Botanical Congress of 13 points about the Code published by a committee convened by T. A. Sprague (1924.03). One point still seems current, "The Rules are too long and complicated." The conference resolved several interesting points: that Latin descriptions should not be required, all later homynyms should be rejected, the type method should be adopted, and duplicate binomials (tautonyms) should be restored.

In Hitchock's reliquiae at US I found two unpublished circulars worth mentioning. One is Hitchcock's circular (six pages, not counting cover letter) to American botanists interested in nomenclature dated 15 October 1924 concerning the practicability of compromise. The other is by Fernald and Weatherby dated 8 December 1924, apparently also widely circulated in America, which discussed the 12 proposals made by Hitchcock. These underlie Hitchcock's compromises (1926.05).

Ithaca Congress of 1926 (4th Congress)

In August 1926, Sprague, Hitchcock, and Briquet showed up at the Ithaca Congress. Sprague's paper was extremely erudite and offered the basis for a world-wide agreement on nomenclature, combining the best features of the International Rules and the Brittonian (American) Code. It is sad that these important proceedings were not published until 1929 (in Duggar).

Hitchcock also made concrete proposals, arguing vigorously for a "standard list of accepted generic names, each with the species that shall direct its application." This would begin with conserved names "but would be gradually extended to include also all generic names in use." This sounds like a precursor of the "names in current use" effort, which is still divided on whether types should be included.

A roundtable discussion was held with papers read by Briquet (review since 1910 with suggestions for the upcoming 1930 Cambridge Congress), Marshall Howe ("I don't feel so irreconcilable as I may have"), and Merritt Lyndon Fernald ("keep Latin"). A paper from N. L. Britton was read for him ("nothing is constant but change"). The report (in Duggar, 1929: 1782) by Karl McKay Wiegand, secretary of the taxonomy section, noted the

approval of an International Interim Committee with John Briquet as chairman, H. Harms, vice-chairman, with more than 20 named members from all over the world. All nomenclatural resolutions were referred to this committee.

Cambridge Congress of 1930 (5th Congress, 3rd Code)

The synopsis of proposals cited 20 documents, most typewritten. One of the most important was a 203-page document (1929.08?) by "British botanists." It included Hitchcock and/or Green's lists of generic names (then 458 currently conserved and 1,159 Linnaean) proposing that the application of these names be controlled by means of the specified "standard-species." Sprague's list of proposed conserved names is the first truly documented approach to proposing names for conservation, hitherto a matter of citing competing names and places of publication (both in proposals and in the Code) and nothing more.

Briquet's synopsis was, as before, a model of clarifying confusion. The multicolumn approach continued, but now with only two columns. The first column had the original text of the Brussels (1912) Code and, in italics in the second column, the rapporteur's comments on the proposed new text. The votes of the Commission on the proposals appeared in a second document "Avis préalable" that was handed out at the Congress (apparently rare).

I will not attempt to summarize or highlight the debates from proceedings beyond saying that the idea of using types to determine the application of names (rather than the original circumscription) was accepted, and the Latin requirement (regarded as arbitrary by Britton) was moved forward from 1908 to 1932. This ended the American schism. There was an interesting discussion (cf. Brooks & Chipp, 1931: 544–553) about matters that since have come to pass or remain needed, such as Harvey Hall's proposed "International Bureau of Plant Taxonomy," making and distributing photographs of types, and producing an index to collections in different herbaria (Ramsbottom).

Unfortunately, John Isaac Briquet died in late October 1931, and the task of producing the third edition of the Code (in three languages) fell to Harms, Rendle, Mangin, Hochreutiner, and Sprague. Sprague (1933) published the main provisions of the amended Code with examples from the British flora. Rendle (1934.06) published an English text (without appendices). The official Cambridge Code appeared about February 1935, only months before the September Amsterdam Congress. The Cambridge Code, despite its extremely short life, was the first completely international Code.

Amsterdam Congress of 1935 (6th Congress)

Briquet's death had delayed the Cambridge Code which, in turn, shortened the lead time for revisions at the next Congress. In September 1934 an announcement appeared in several journals (*J. Bot.* and *Bull. Misc. Inform.*) that proposals to amend the (still unpublished) Code had to be submitted in 100 copies by 1 January 1935. (That should slow things down!) Nonetheless, indefatigable botanists produced 14 submissions and, by July 1935, Sprague sent the synopsis of proposals to the seven members of the Executive Committee of Nomenclature elected at Cambridge and to seven others, obtaining 10 votes. These were used to compile the Preliminary Opinions distributed at the Congress in September.

Among the submissions processed by Sprague, I have had most occasion to consult the 43 collected proposals "by twelve botanists" that appeared in 1935.03. I would draw attention to Wilmott's *Index Purgatio*, listing works that should be rejected for various cited reasons, and Sprague and Green's provisional list of institutions in 20 geographical areas to get copies to validate names.

English now became the official language, replacing French, which had been official since Britton's proposal to the 1905 Vienna Congress was approved. The preceding Brussels and Cambridge proceedings had been reported in French, but problems arose with the unexpected death of Briquet. Harms, the vice-rapporteur, asked Rendle to prepare the English text since most of the proposals had been in English. The French and German texts were generated by translation from Rendle's English text. Sprague thanked Miss Mary Letitia "Manna" Green for her collaboration (in fact, he married her).

Sprague asked that the 1935 Cambridge Code be recognized as a faithful record of the 1930 Cambridge decisions. This was wise in view of the great difficulties after Briquet's death, and it would have been even more futile than usual for nomenclaturalists to argue whether or not a proposal had been implemented correctly. He did ask that the Latin requirement date be moved forward again, from 1932 (when the Code had been expected) to 1935 (when the Code came out). He also proposed automatic rejection of proposals with less than 20% support in the preliminary (Commission) vote.

Probably the major battle of this Congress concerned the application of a combination when mis-

applied, the classic example being *Tsuga mertensiana* (Bong.) Carr. Carrière based his name on Bongard's *Pinus mertensiana* but applied it to an excellent illustration that was not Bongard's species. This is a classic problem of the old circumscription method tangling with the new type method (just introduced), not to mention the whole question of whether or not parenthetic authors should be cited that had so vexed nomenclaturalists of the preceding century.

Hitchcock died on shipboard while returning from the Amsterdam Congress.

Now World War II interposed. Not only was there no Stockholm Congress in 1940, there never was an official Amsterdam Code. Until the next Congress (Stockholm in 1950) people had to make do with 1935 (Cambridge) Code and what they could find about the Amsterdam Congress (fortunately not too drastically changed, but the type method was new to many) mostly from Sprague's summary in 1936 and the Congress proceedings. Approved conserved names were listed by Sprague (1940.06).

Brittonia Code (Unofficial)

In the late 1940s steps were taken to revive things, just as after World War I. The word went out in 1946 that there would be a Congress in Stockholm in 1950. In March 1946 the Council of the American Society of Plant Taxonomists appointed a committee (Camp, Rickett, and Weatherby) to prepare for the Congress. They produced the unofficial "Brittonia" Code (1947.04), followed by a symposium on botanical nomenclature in December 1947 at St. Louis (published 1949.01). Weatherby's paper, "Botanical nomenclature since 1867," said everything that should be said.

Meanwhile, in February 1947, Professor Lanjouw (Utrecht) wrote to several botanists and, having gotten support, invited taxonomists to a June 1948 conference on preparing a new Code. The results were not published until August(?) 1950 but they had dramatic consequences before. Among the Americans at the Utrecht Conference were Merrill and Rickett, who were already involved in the American initiative. Ray Fosberg was there (and attended the thesis defense of Frans A. Stafleu). Lanjouw agreed to be acting rapporteur général, succeeding Sprague.

Stockholm Congress of 1950
(7th Congress, 4th Code)

Lanjouw's synopsis of proposals was large (255 pages) and was mailed with the first voting form, requesting return by 1 June 1950. I note that A. C. Smith received his copy on 5 June, so he did not return it. There were *only* 540 proposals to process in 40 hours (4 minutes each). Two hundred mail ballots were received and anything with less than 25% support was automatically rejected.

An important event occurred on 18 July 1950 at what Stafleu (1988.08: 795) called "an informal session" (attended by 130 taxonomists). Lanjouw's proposals for an association with an office (bureau) in Utrecht was accepted and became Resolution 10 of the Congress (pp. 67, 68). This was the official beginning that turned into things like the *Taxon* and *Regnum Vegetabile*. *Taxon*, being the official journal of the new International Association for Plant Taxonomy, became the vehicle for proposals to amend the Code so that they no longer were scattered through the literature. I would be astonished if any working taxonomist does not consult something in *Regnum Vegetabile* almost every day, be it *Index Herbariorum*, *TL-2*, *ING*, or even the *Code*.

The first issue of *Taxon* appeared in September 1951. The first issue of *Regnum Vegetabile* (actually numbered 3) was the Stockholm Code, which appeared in September 1952, barely in time for the Paris Congress. The editing of the Stockholm Code was described by Merrill (1952.01). The Stockholm Congress proceedings came out in 1953.

Paris Congress of 1954
(8th Congress, 5th Code)

This was the first Congress to have all proposals published in a single journal. The Geneva Conference of 25–30 January 1954 was a precursor event, as the Utrecht Conference of June 1948 before the Stockholm Congress. Its report appeared in April 1954, soon after the synopsis. Stafleu's report on the proceedings appeared in August 1955. A feature of the 1956 (Paris) Code was the appearance of a fourth language, Spanish. Another was a concordance of Article and Recommendation numbers among the latest Paris Code and the two preceding Codes (Stockholm and Cambridge).

It would be useful to extend this concordance back through the three preceding Codes, Brussels (1912), Vienna (1906), and Paris (1867). Somehow this should then weave in all proposals to the same text (including rejected ones) and the examples proffered. I am convinced we would find we are constantly reinventing the wheel, if not repeatedly raising the same examples discussed before.

There is neither time nor space to continue since

we are only half way through and have six more Codes to go, the products of the subsequent Congresses: Montreal (1959), Edinburgh (1964), Seattle (1969), Leningrad (1975), Sydney (1981), and Berlin (1987). Montreal was my first Congress and I was somewhat distracted by being on my honeymoon. My best memory of Edinburgh was the "Bloody Donk" speech. At Seattle I made my first motion on the floor (defeated) and have been told that this was the last "decent" Code. Leningrad passed my orthography proposals, probably assisted by my absence when discussions started, for the first time, with proposals pertaining to the last articles of the Code. This was the first Code to number paragraphs within articles, making it easier to cite. Sydney was the first Congress most of us experienced without Stafleu in the chair and "mice will play when the cat is away." Stafleu rejoined us for Berlin (1987), but said that he will not go to Tokyo (1993).

We must end on an upbeat, and I can do no better than repeat Weatherby's (1949.01: 7) translated quotation from Alphonse de Candolle's introduction to his 1867 *Lois* (with a few minor changes since nomenclaturalists can't even quote each other without making "improvements"): "There will come a time when all the plant forms in existence will have been described; when herbaria will contain indubitable material of them; when botanists will have made, unmade, often remade, raised or lowered, and above all, modified several hundred thousand taxa ranging from classes to simple varieties, and when synonyms will have become much more numerous than accepted taxa. Then science will have need of some great renovation of its formulae. This nomenclature which we now strive to improve will then appear like an old scaffolding, laboriously patched together and surrounded and encumbered by the debris of rejected parts. The edifice of science will have been built, but the rubbish incident to its construction not cleared away. Then perhaps there will arise something wholly different from Linnaean nomenclature, something so designed as to give certain and definite names to certain and definite taxa.

"That is the secret of the future, a future still very far off.

"In the meantime, let us perfect the binomial system introduced by Linnaeus. Let us try to adapt it better to the continual, necessary changes in science . . . drive out small abuses, the little negligences and, if possible, come to agreement on controversial points. Thus we shall prepare the way for the better progress of taxonomy."

Chronologic Bibliography on Botanical Nomenclature, With Some Annotations

The entries in this bibliography are arranged chronologically to better reflect the subject, history. The bibliography's purpose is not just to support text references as conventional Literature Cited, and it has unexpected entries such as the death date of some critical workers.

All citations appear with the date in the format year.month.day, i.e., in increasing degrees of accuracy. Incompletely dated publications are usually cited after more completely dated publications. Some publications give only a spread of months, such as (06–07), or days 10–17. The query (?) was used when there is more than usual uncertainty. Dates were mostly determined from evidence in the publications or from other sources, such as Stafleu and Cowan's *Taxonomic Literature II.*

1737.07. Linnaeus, C. Critica Botanica. 270 pp. Lugduni Batavorum. [Arthur Hort's translation, revised by M. L. Green, published 1938 by the Ray Society, was questioned by Heller (1964.04). Note: As Miss Green said, when Linnaeus spoke of specific names, he meant the diagnostic phrases in the binary system of his predecessors and himself, not the trivial epithets later adopted in his binomial system.]

1753.05.01. Linnaeus, C. Species Plantarum . . . . Holmiae.

1798.11. Lamarck, J. B. A. P. Monnet de. Nomenclature. Pp. 498–499 *in* Encycl. Meth. Bot. Volume 4. H. Agasse, Paris. [Complained of abuses, such as Linnaeus's converting *Syringa* into *Philadelphus*, opposing the replacement of names familiar to botanists. "These two kinds of names [generic and specific] ought to be subject to rules that cannot be set aside without prejudicing the science that they aim to facilitate." He particularly objected to the generic names of the Forsters. He objected to specific epithets that are untrue and those derived from names of places or scholars (the latter were OK for genera).]

1813. Candolle, A. P. de. De la nomenclature. Pp. 221–252 *in* Théorie Élémentaire de la Botanique . . . . Paris.

1821.01. Smith, J. E. Respecting Nomenclature . . . . Pp. 51–54 *in* A Grammar of Botany. Longman et al., London. Reprinted by Prakash Publishers, Jaipur, in 1973. [Objected to corrupt names. "Future general writers on Botany, of competent authority, must reform these abuses."]

1832.10. Lindley, J. An Introduction to Botany . . . . Longman et al., London. [Chapter IV of Nomenclature and Terminology (pp. 454–459) and V Of Synonyms (pp. 460–462). DC. uses asteriks (*) in synonymy = good description. "Mark of admiration" (!) indicates inspection of authentic specimen—thus, "Linn.!. sp. pl. 427."]

1843. Strickland, H. E. (reporter), J. Phillips, J. Richardson, R. Owen, L. Jenyns, W. J. Broderip, J. S. Henslow, W. E. Shuckard, G. R. Waterhouse, W. Yarrell, C. Darwin & J. O. Westwood. Series of propositions for rendering the nomenclature of zoology uniform and permanent. Report of the 12th Meeting of the British Association for the Advancement of Science held at Manchester in June 1842, pp. 105–121.

1843.07. Gould, A. A. Notice of some works, recently

published, on the nomenclature of zoology. Amer. J. Sci. Arts 45: 1–12.

1860. STIMPSON, W. On botanical and zoological nomenclature. Edinburgh New Philos. J. 12: 321–324.

1864.03. GRAY, A. Nomenclature. Amer. J. Sci. Arts, ser. 2, 37: 279–281. [Commented on the newly reprinted zoological rules (Edinburgh New Philos. J. 1863: 260–).]

1866.06.01. KOCH, K. Some propositions with respect to systematic botany. J. Bot. 4: 201. [Abstract, translated from German.]

1866.?? KOCH, K. Einige die Systematik betreffende Vorschläge. Pp. 188–195 *in* [Secretary?], Int. Hort. Exhib. Bot. Congr. London 22–31 May 1866 Rep. Proc. [total pagination?] Truscott, Son & Simon, London. [English summary appeared on pp. 21–22.]

1866.12.01. [SEEMANN, B.?] [Review of] Prodromus Naturalis Regni Vegetabilis. Editore A. de Candolle. Pars. XV., Sectio Posterior, Fasc. II. Sistens Euphorbiaceas. Auctore J. Müller, Argoviensi. Paris. 1866. J. Bot. 4: 387–388. [Objection: ". . . because he includes forms that had before been excluded, he displaces the name of the author of the species, and attaches his own to it."]

1867.01. GRAY, A. An innovation in nomenclature in the recently-issued volumes of the "Prodromus." Amer. J. Sci. Arts, ser. 2, 43: 126–128. [Objected to J. Mueller changing the authorship of generic names when changing the circumscription.] [Reprinted by Seemann: J. Bot. 5: 81–84. 1867.03.01.]

1867.05.01. CANDOLLE, A. L. DE. [Correspondence concerning criticisms of] Dr. Mueller's Monograph of the Euphorbiaceae. J. Bot. 5: 151–152.

1867.08.01. CANDOLLE, A. L. DE. Lois de la Nomenclature botanique redigées et commentées . . . . 60 pp. V. Masson et fils, Paris. [Basis for discussion.]

1867.09.12. CANDOLLE, A. L. DE. Lois de la Nomenclature botanique adopteés par le Congrès . . . a Paris en Août 1867 . . . . 64 pp. H. Georg, Genève et Bâle, J. B. Bailliére et fils, Paris.

1867.11. CANDOLLE, A. L. DE (RAPPORTEUR). Discussion des Lois de la Nomenclature botanique. Pp. 177–208 [and] Lois de la Nomenclature botanique. Pp. 209–255 *in* E. Fourneri (Secrétaire), Actes du Congrès International de Botanique . . . . Paris.

1867.12. CRÉPIN, F. La Nomenclature botanique au Congrès internationale de Botanique. 28 pp. [The author citation argument ad nauseam.]

1868. DES MOULINS, C. Lettre à Monsieur François Crépin. 10 pp. Bordeaux. [Reprinted from Actes Soc. Linn. Bordeaux 26(4).]

1868.?? CANDOLLE, A. L. DE. Laws of Botanical Nomenclature. [English translation] by H. A. Weddell. 72 pp. L. Reeve & Co., London.

1868.07. GRAY, A. Editorial remarks and suggestions [on the laws of botanical nomenclature.] Amer. J. Sci. Arts, ser. 2, 46: 74–77. [Preceded (pp. 66–74) by a copy of Weddell's English translation.]

1869.06. CANDOLLE, A. L. DE. Réponse à diverses questions et critiques faites sur le Recueil des *Lois de Nomenclature botanique*, tel que le Congrès international de 1867 l'a publié. Bull. Soc. Bot. France 16: 64–81.

1870.01? CARUEL, T. & A. L. DE CANDOLLE. [Correspondence.] Una questione di nomenclatura botanica. Nuovo Giorn. Bot. Ital. 2: 146–149. [Names published with a query.]

1874.02–04. MÜLLER, J. Nomenclatorische Fragmente [with six parts.] Flora 57: 89–94; 119–126; 156–159. [Motion 1 in Briquet (1905.03.15: 7).]

I. Ueber die Gültigkeitsbedingungen der systematischen Namen. Pp. 89–94.

II. Ueber das Citiren der Autoren bei generisch neu gestellten Arten. Pp. 119–121.

III. Ueber die Autorität bei verwendeten Zettelnamen. Pp. 121–123.

IV. Ueber das Autorschema bei umgeänderten Gattungsbegriffen. Pp. 123–126.

V. Ueber das Ableiten der Speciesnamen von Varietätsnamen. P. 156.

VI. Verliert ein systematischer Name seinem Rang so verliert er zugleich sein Prioritätsrecht. Pp. 156–159.

1875.01. ČELAKOVSKY, L. Zwei Fragen der botanischen Nomenclatur. Flora 58: 2–6; 21–31. [Priority right of species epithets and generic names.]

1876.12? COGNIAUX, C. A. & A. L. DE CANDOLLE. [Correspondence.] Quelques points de nomenclature botanique. Bull. Soc. Roy. Bot. Belgique 15: 477–485. [First appearance of the principle "Never attribute to an author what he didn't say."]

1877.06. TRIMEN, H. Some points in botanical nomenclature. J. Bot. 15: 189–190. [Supports de Candolle's position in the published Cogniaux correspondence (1876.12?). First mention of what will be known as Kew Rule on p. 190.]

1877.08. CANDOLLE, A. L. DE. [Letter & response by editor, Trimen.] J. Bot. 15: 242–243. [Opposing the Kew Rule; defended by Trimen.]

1877.09. CARUEL, T. Botanical nomenclature. J. Bot. 15: 282. [Supported Kew Rule as espoused by Trimen's response to de Candolle (1877.08).]

1877.10. CARUEL, T. Divisiones plantarum propositae. Nuovo Giorn. Bot. Ital. P: 280–281. [Phanerogamae, Schistogamae, Prothallogamae, Bryogamae & Gymnogamae.]

1877.12. BALL, J. On some questions of botanical nomenclature. J. Bot. 15: 357–360. [Supported de Candolle (1877.08), opposing the Kew Rule.]

1877.12. DALL, W. H. Nomenclature in zoology and botany. A report to the American Association for the Advancement of Science at the Nashville Meeting, August 31, 1877. 56 pp. (A.A.A.S., Volume XXVI). [Important survey of zoologists and Code with elements for botanists.]

1878.03. HIERN, W. P. On a question of botanical nomenclature. J. Bot. 16: 72–74. [Supports the Kew Rule.]

1878.05. BALL, J. On disputed questions of botanical nomenclature. J. Bot. 16: 140–142. [Balanced discussion of Kew Rule, basically opposing it.]

1878.06. TRIMEN, H. On a point in botanical nomenclature. J. Bot. 16: 170–173. [". . . the framing of a fixed rule . . . . This practice is, to employ the earliest published name the generic half of which is the name of the genus adopted, and thus avoid making a new [binomial] name by the resuscitation of the specific half of an older combination."]

1878.09. MATHEWS, W. Botanical nomenclature. J. Bot. 16: 260–262. [Advocated the zoological method of author citation.]

1878.11. Candolle, A. L. de. Botanical nomenclature. J. Bot. 16: 345–346. [Drew attention to his upcoming Supplément (1883.07?), subsequently excerpted in English by Britten (1888.10).]

1878.12. Bentham, G. Nomenclature. Pp. 189–198 [in his] Notes on Euphorbiaceae. J. Linn. Soc., Bot. 17: 185–267. [Objected to those who have abandoned "the rules that long-established custom amounts to prescription . . . ," i.e., when priority should be set aside, as for Patrick Browne, but accepted Adanson. Opposed "correcting" original spellings. Supported what will be the Kew Rule. Excerpted by J. Bot. 17: 45–48. 1879.01.]

1879.04. Gray, A. Review of Bentham's "Notes on Euphorbiaceae." Amer. J. Sci. Arts [Extracted by: Bot. Gaz. (Crawfordsville) 4: 158–161. 1879.05; J. Bot. 18: 186. 1880.06.]

1879.07. Coulter, J. M. & M. S. Coulter. Honorary names in scientific nomenclature. Bot. Gaz. (Crawfordsville) 3: 61–64. [Provoked by *Gilia parreyae*: discriminates between possessive (in genitive) and dedicative (adjectival) epithets. Worshipful of Asa Gray.]

1879.08.01. Müller, F. von. Einige Worte über die erste Ausgabe von Linné's Species Plantarum in Bezug auf Vorzugsrecht. Bot. Zeig. (Berlin) 37: 490–491.

1879.08.01. Drude, O. Über Nomenclaturfragen. Bot. Zeit. (Berlin) 37: 492–494.

1880.03? Saint-Lager, J. B. Réforme de la nomenclature botanique. Ann. Soc. Bot. Lyon 7: 1–154.

1. Origines de la Nomenclature [incl. Nomenclature des Grecs.]. Pp. 1–37.
2. Réforme des épithètes spécifiques qui ne s'accordent pas avec le nom générique. Pp. 38–60.
3. Réforme des épithètes spécifiques qui forment pléonasme avec le nom générique. Pp. 61–66.
4. Réforme des noms composés d'un radical grec associé à un radical latin. Pp. 67–72.
5. La Nomenclature botanique est formée de noms grecs et latins. Pp. 73–75.
6. De la désinence des noms génériques. Pp. 76–111. [With lists of ancient Greek names kept without change of inflection, with changes, modern names with two Greek stems of which the last is masculine, neuter, and feminine.]
7. De la désinence des épithètes spécifiques. Pp. 112–138.
8. Des épithètes spécifiques barbares [or based on a person's name, or banal, geographic or recalling industrial or medicinal properties]. Pp. 139–150.
9. Conclusions. Pp. 151–154.

1881.04. Saint-Lager, J. B. Nouvelles remarques sur la nomenclature botanique. Ann. Soc. Bot. Lyon 8: 149–203.

1. Du genre grammatical des mots "Lotos et Melilotos." Pp. 149–156.
2. De la désinence des noms de genre. Pp. 156–163.
3. Remarques sur le genre grammatical des noms génériques d'origine grecque. Pp. 164–169.
4. Des noms de genre tirés d'un nom d'homme. Pp. 170–178.
5. Orthographe de quelques noms de genre. Pp. 179–183.
6. Des pléonasmes. Pp. 184–188.
7. Des noms composés. Pp. 188–190.
8. L'adjectif s'accorde avec le substantif auquel il se rapporte. Pp. 191–203.
9. "Medice, cura te ipsum." [Corrections to this and preceding work.] P. 203.

1881.03. Jackson, B. D. On some recent tendencies in botanical nomenclature. J. Bot. 19: 74–83. [Objected to parenthetic author citations, "corrections," faulty capitalizing of species epithets, and mischievous author abbreviations.]

1882.06. Gray, A. The citation of botanical authorities, J. Bot. 20: 173–174. [Advocated crediting names in Aiton's Hort. Kew. to Aiton, not Solander, R. Brown, etc.]

1883.07? Candolle, A. L. de. Nouvelles remarques sur la nomenclature botanique . . . . Supplément au commentaire du même auteur qui accompagnait le texte des lois. 79 pp. H. Georg, Genève. [Motion 2 in Briquet (1905.03.15: 7); Motion 1 in Briquet (1910.04?: 1).]

1883.10.31. Bubani, P. Su di alcune divergenze intorno la nomenclatura botanica . . . ed il compilatore delle proteste Leggi Prof. Alf. de Candolle. 15 pp. Bologna. [Objected to the tyranny of laws.]

1883.12. Gray, A. Some points in botanical nomenclature; a review of "Nouvelles Remarques sur la Nomenclature Botanique, par. M. Alph. de Candolle," Geneva. 1883. Amer. J. Sci. Arts, ser. 3, 26: 417–437.

1887.03. Jackson, B. D. A new "Index of plant-names." J. Bot. 25: 66–71 (Jan.); 150–151 (May). [Kew Rule spelled out on p. 69. Statement from J. Hooker about the origin of the Index.]

1887.06. Wittmack, L. Règles à suivre pour la nomenclaturae des plantes en général, et des Orchidées en particulier (5e question au Congrès de 1887). J. Soc. Natl. Hort. France ser. 3, 9: cvii–cxxiii. [Seen as 16 pp. reprint.]

1887.10. Greene, E. L. The permanency of specific names. J. Bot. 25: 301–303. [Objected to the Kew Rule.]

1887.12. Gray, A. Botanical nomenclature. J. Bot. 25: 353–355. [Attacked Greene by quoting Bentham and supported the Kew Rule.]

1888.01. Asa Gray died at 78.

1888.04. Poggenberg, J. F., N. L. Britton, E. E. Sterns, A. Brown, T. C. Porter & A. Hollick (committee of torrey botanical club). Preliminary catalogue of Anthophyta and Pteridophyta reported as growing spontaneously within one hundred miles of New York City. 90 pp. [Nomenclature by Britton, Sterns & Poggenberg (subcommittee), beginning of the Brittonian (American) schism.]

1888.06. Greene, E. L. Botanical literature, old and new. Pittonia 1: 176–194. [177–183 reviews a Ray 1660 publication with 48 binomials. 184–194 reviews the new preliminary catalogue by Poggenberg et al.]

1888.09. Britten, J. Recent tendencies in American botanical nomenclature. J. Bot. 26: 257–262. [Objected to Britton, Sterns & Poggenberg overturning the Kew Rule.]

1888.09. Sterns, E. E. The nomenclature question and how to settle it. Bull. Torrey Bot. Club 15: 230–235.

1888.10. Candolle, A. L. de. [Letter concerning] Botanical nomenclature. J. Bot. 26: 289. [Agreed with Britten's (1888.09) protest about Britton et al. and

complimented Asa Gray, about whom Americans ought to be proud and follow. Opposed the Kew Rule.]

1888.10. BRITTEN, J. Translation of Art. 48 discussion in A. L. de Candolle's "Nouvelles Remarques." J. Bot. 26: 290–292.

1888.10. BRITTON, N. L. [Response to Britten's protest of 1888.09.] J. Bot. 26: 292–295. [Argued that he only did what Elias Fries, Boissier, Richard Spruce, and a host of others have done (he was wrong about Boissier, who was strictly Candollean).]

1891. NORDSTEDT, O. Om originalexemplars betydelse vid prioritetsfrågor. Bot. Not. 1891: 76–82.

1891.10. KUNTZE, O. Revisio Generum Plantarum . . . . Volume 1–2. 1011 pp. (+ 155 introduction). [A bomb with thousands of new names and combinations. The chapter "Abänderungsvorschläge nebst Motiven zu den internationalen botanischen Nomenclatur-Regeln von 1867," pp. lxxvi–cxxii, accepted as Motion 3 in Briquet (1905.03.15: 7) and as Motion 2 in Briquet (1910.04?: 1).]

1891.11.27. DRUDE, O. Bemerkungen zu Dr. Otto Kuntze's Aenderungen der systematische Nomenclatur. Ber. Deutsch. Bot. Ges. 9: 300–306.

1892.02.04. BRIQUET, J. Zur generischen Nomenclatur der Labiaten. Bot. Centralbl. 49: 106–111. [Briquet's maiden nomenclatural paper, what Kuntze did to mints.]

1892.05. CANDOLLE, A. L. DE. A note on nomenclature. J. Bot. 30: 135. [Noted Briquet's evidence against Kuntze's changes of Labiates and avowed great pleasure "dans mes vieux jours" with the support of principles he had always espoused.]

1892.07? MALINVAUD, E. Quatre propositions relatives a la nomenclature émises par un Comité de botanistes de Berlin; lettre d'approbation de M. Alphonse de Candolle. Bull. Soc. Bot. France 39: 137–142. [De Candolle's letter was dated 6 July 1892, one of his last published comments on nomenclature.]

1892.07. ASCHERSON, P. Vorläufiger Bericht über die von Berliner Botanikern unternommenen Schritte zur Ergänzung der "Lois de la nomenclature botanique." Ber. Deutsch. Bot. Ges. 10: 327–359. [Four Resolutions. English J. Bot. 30: 241–242. 1892.08. Motion 4 in Briquet (1905.03.15: 7).]

1892.08? GREENE, E. L. Dr. Kuntze and his reviewers. Pittonia 2: 263–281. [Reprinted in Chron. Bot. 12: 249–257. 1951.09. Statement by one of Kuntze's strongest supporters.]

1892.09. FAIRCHILD, D. G. (SECR.). Proceedings of the Botanical Club of the Forty-first Meeting of the A.A.A.S., Rochester, New York, August 18–24, 1892. Bull. Torrey Bot. Club 19: 281–297. [Pp. 290–292 have the Rochester resolutions signed by N. L. Britton, J. M. Coulter, H. H. Rusby, W. A. Kellerman, F. V. Coville, L. M. Underwood & L. F. Ward (Committee on Botanical Nomenclature). Motion 5 in Briquet (1905.03.15: 7).]

1892.11.15. UNDERWOOD, L. M. The nomenclature question at Genoa. Bull. Torrey Bot. Club 19: 324–330.

1892.11. UNDERWOOD, L. M. The International Congress at Genoa. Bot. Gaz. (Crawfordsville) 17: 341–347.

1893.07?–10? KUNTZE, O. Die Bewegung in der botanischen Nomenclatur von Ende 1891 bis Mai 1893. Bot. Centralbl. 54: 353–361; 385–408.

1893.04.04. Alphonse de Candolle died at 86.

1893.04? PENZIG, O. (SECR.). Quarta adunanza, Martedì 6 Settembre alle 2 pom. Atti del Congresso Botanico Internazionale di Genova 1892. 81–126 [International Commission to consider four proposals of Berlin botanists announced on 9 Sep. pp. 439–440. Pp. 117–121 accepted as Motion 7 by Briquet (1905.03.15: 7). Holmes's emendations in botanical terminology (pp. 121–124) accepted as Motion 8 by Briquet (1905.03.15: 7).]

1893. ASCHERSON, P. Die Nomenclaturbewegung von 1892. Bot. Jahrb. 15(Beibl. 38): 20–28. [Also in Ber. Pharmac. Ges. 4: 35–45. 1894.]

1893.06. JACKSON, B. D. Index Kewensis. 1st fascicle [2nd fascicle in December.]

1893.07. KUNTZE, O. Revisio Generum Plantarum 3(1): clx–ccccxxii. [Codex nomenclaturae botanicae emendatus (pp. ccclxxxv–cccxvi) accepted as Motion 9 in Briquet (1905.03.15: 8) and as Motion 3 in Briquet (1910.04?: 1).]

1893.09. SWINGLE, W. T. (SECR.). Proceedings of the Botanical Club, A.A.A.S., Madison meeting. Bot. Gaz. (Crawfordsville) 18: 342–349. [Pp. 342–343 accepted as Motion 10, without Art. II, by Briquet (1905.03.15: 8), also Britton's report of same date.]

1893.09. BRITTON, N. L. Proceedings of the Botanical Club, A.A.A.S., Madison meeting, August 18–22, 1893. Bull. Torrey Bot. Club 20: 360–365. [Pp. 360–361 accepted as Motion 10, without Art. II, by Briquet (1905.03.15: 8), also Swingle's report of same date.]

1893? Om en fälles Nomenclatur i systematik Botanik for Skandinavien. Förh. Skand. Naturf. 14 Moede 1892: 240–255. [Motion 6 in Briquet (1905.03.15: 7). Not seen.]

1893. Fraen Botaniska Sällskapets i Stockholm förhandlingar. Bot. Not. 1893: 158–161. [Motion 11 in Briquet (1905.03.15: 8). Not seen.]

1894.02. BRIQUET, J. Questions de nomenclature. Bull. Herb. Boissier 2: 49–88. [Motion 12 by Briquet (1905.03.15: 8).]

1894.07. KUNTZE, O. Nomenclatur-Studien. Bull. Herb. Boissier 2: 456–498.

1894.12.28. KNOBLAUCH, E. Die Nomenclatur der Gattungen und Arten. Bot. Centralbl. 61: 1–6. [Motion 13 in Briquet (1905.03.15: 8).]

1895.01.15. BARNHART, J. H. Family nomenclature. Bull. Torrey Bot. Club 22: 1–24. [Important document (see author's mature comment 1922.09). Motion 14 in Briquet (1905.03.15: 8).]

1895.01. ASCHERSON, P. & A. ENGLER. Erklärung der Geschäftsleitung der vom internationalen botanischen Congress zu Genua (1892) eingesetzen Nomenclatur-Commission. Oesterr. Bot. Z. 45(1): 27–35. [Motion 15 in Briquet (1905.03.15: 8 as pp. 327–335). Also in Verh. Ges. Deutsch. Naturf. 2: 153–159. 1894?]

1895.03. ROBINSON, B. L. On the "List of Pteridophyta and Spermatophyta of Northeastern America," prepared by the Nomenclature Committee of the Botanical Club. Bot. Gaz. (Crawfordsville) 20: 97–103.

1895.04. COVILLE, F. V. A reply to Dr. Robinson's criticism of the "List of Pteridophyta and Spermatophyta of Northeastern America." Bot. Gaz. (Crawfordsville) 20: 162–167.

1895.04.13. PFITZER, E. Beiträge zur Systematik der Orchideen. I. Zur Nomenclatur. Bot. Jahrb. 19: 1–28. [What Kuntze did to orchids.]

1895.05? KUNTZE, O. Bemerkungen zum künftigen bo-

tanischen Nomenclatur-Congress. 5 pp. [Reprinted from Oesterr. Bot. Z. 1895(5): ??–??, not seen.]
1895.06. Robinson, B. L. On the application of "once a synonym always a synonym" to binomials [with a circular letter extract: Recommendations regarding the nomenclature of systematic botany.] Bot. Gaz. (Crawfordsville) 20: 261–263.
1895.07. Coville, F. V. Dr. Robinson and homonyms. Bot. Gaz. (Crawfordsville) 20: 320–322.
1895.07? Smith, E. F. The Botanical Club CheckList: A protest. [Published by author?] 16 pp.
1895.07. Ward, L. F. The nomenclature question. Bull. Torrey Bot. Club 22: 308–329. [Survey of history of nomenclature and plea for peace.]
1895.08. Anderson, C. L. & 73 Other American Botanists. Recommendations regarding the nomenclature of systematic botany. Bot. Jahrb. 21 (Beibl. 52): 12–15. [The Britton school's loyal opposition, called the Harvard Code.]
1895.08. Robinson, B. L. A further discussion of the Madison rules. Bot. Gaz. (Crawfordsville) 20: 370–371.
1895.09. Orcutt, C. R. Nomenclature. Out of Doors for Women 3(22): 1–2. [*Mam(m)illaria* vs. *Cactus*.]
1895.11. Kuntze, O. Les besoins de la nomenclature botanique. Monde Pl. [Seen only as 6-page reprint: lays out what Congress should do and hopes to complete a "Nomenclator plantarum omnium correctus" by 1905.]
1895.11. Thistleton-Dyer, W. Nomenclature. Bull. Misc. Inform. 1895: 278–281. [P. 280, "To me the botanists who waste their time over priority are like boys who, when sent on an errand, spend their time in playing by the roadside."]
1895. Malinvaud, L. J. E. La loi de priorité dans la nomenclature botanique. Congrès de Bordeaux. Assoc. Franç. l'Advancem. Sci. 4 pp. [Seen as reprint. Gave examples in *Alyssum* and *Carex* that seem unexceptional by today's standards.]
1896.02. Various Authors. The nomenclature question. Bot. Gaz. (Crawfordsville) 21: 82–91.
1. knowlton, f. h. Some inconsistencies in plant nomenclature. pp. 82–85.
2. davenport, g. e. Botanical nomenclature. Pp. 85–88.
3. kuntze, o. Some remarks on nomenclature. Pp. 88–90.
4. meehan, t. Dates and references, and priority in nomenclature. Pp. 90–91.

1896. Le Jolis, A. Lettre . . . a M. Malinvaud. Bull. Soc. Bot. France 42: 661–663.
1896.04.12. Buchenau, F. G. P. [Untitled.] Bot. Jahrb. 24: 648–668. [Comment on nomenclatural issues.]
1896.06. Levier, É. La pseudo-priorité et les noms a béquilles. Bull. Herb. Boissier 4: 369–406. [Attack on Kuntze's work.]
1896.08. Briquet, J. Questions de nomenclature. 14 pp. [Reprinted from Observations préliminaires. *In:* E. Burnat's Flore des Alpes maritimes. 2: v–xvi.]
1896.12.01. Garcke, A. Einige nomenclatorische Bemerkungen. Bot. Jahrb. 22(Beibl. 55): 1–10.
1897.05. Harms, H. Die Nomenclaturbewegung der letzten Jahre. Bot. Jahrb. 23(Beibl. 56): 1–32.
1897.06 [separate says 8 Mai]. Engler, A., I. Urban, A. Garcke, K. Schumann, G. Hieronymus, P. Hennings, M. Gürke, U. Dammer, G. Lindau, E. Gilg, H. Harms, P. Graebner, G. Volkens & L. Diels. Nomenclaturregeln für die Beamten des Königlichen Botanischen Gartens und Museums zu Berlin. Notizbl. Königl. Bot. Gart. Berlin 1: 245–250. [The Berlin Code. Motion 16 in Briquet (1905.03.15: 8). Also in Gartenflora 46: 304–308. 1897.06.01, which Robinson (1897.08) translated into English.]
1897.08. Britton, N. L. [Translation and comments on] Nomenclaturregeln für die Beamten . . . zu Berlin. Bull. Torrey Bot. Club 24: 415–419.
1897.08. Robinson, B. L. The official nomenclature of the Royal Botanical Garden and Museum of Berlin. Bot. Gaz. (Crawfordsville) 24: 107–110.
1897.08. Britten, J. The Berlin Rules for nomenclature. J. Bot. 35: 305–307.
1897.08.25. Kuntze, O. Levier's Verdrehung von Artikel 49 des Pariser Codex. Bot. Centralbl. 71: 302–305. [Protests twisting of the Code.]
1897.09. Briquet, J. "Règles de Nomenclature pour les botanists attachés au Jardin et au Musée royaux de Botanique de Berlin" traduites et suives d'observations critiques. Bull. Herb. Boissier 5: 768–779.
1898.02. Engler, A. Anacardiaceae africanae. II. Bot. Jahrb. 24: 493–502. [Provoked Britten, 1898.03.]
1898.03. Britten, J. The fifty years' limit in nomenclature. J. Bot. 36: 90–94. [*Odina* vs. *Lannea* vs. *Calesiam* vs. *Haberlia*.]
1898.06. Robinson, B. L. Some reasons why the Rochester Nomenclature cannot be regarded as a consistent or stable system. Bot. Gaz. (Crawfordsville) 25: 437–445.
1898.08.12. Cook, O. F. Stability in generic nomenclature. Science n.s. 8: 186–190. [Comments on Robinson, 1898.06.]
1898.09. Kuntze, O. Revisio Generum Plantarum. [Last two parts of 3rd volume. Part 2: 163–167, 180–201, "Codex nomenclaturae emendatus, supplementum" accepted as Motion 17 in Briquet (1905.03.15: 8) and in Briquet (1910.04?: 1).]
1898.10.29. Le Jolis, A. Protestation contre le Reviso generum plantarum III[II]. 11 pages. J. Mersch imp., Paris. [Reprinted from J. Bot. (Morot) 12.]
1898. Greene, E. L. Bibliographical difficulties in botany. Catholic Univ. Bull. 4: 62–75. [Presentation of the circumscription method for determining the application of names.]
1898. Levier, E. Le cas du Docteur Otto Kuntze. 12 pp. Florence. [Satiric, pungent, and delightful criticism of Kuntze's arguments and efforts.]
1899.02.08. Kuntze, O. Protest gegen die Schweinfurth'sche Erklärung. Bot. Centralbl. 77: 259–262.
1899.05.10–17. Čelakovsky, L. J. Das Prioritätsgesetz in der botanischen Nomenclatur. Bot. Centralbl. 78: 225–234, 258–268.
1899.09.15. Engler, A. et al. Erklärung. Bot. Jahrb. 27 (Beibl. 63): 7. [In reference to Engler et al. (1897.06). Motion 18 in Briquet (1905.03.15: 8).]
1899.09.20. Kuntze, O. Ueber neue nomenclatorische Aeusserungen. Bot. Centralbl. 79: 405–412.
1899.12. Underwood, L. M. Review of the genera of ferns proposed prior to 1832. Mem. Torrey Bot. Club 6: 247–283. [Not seen, generic typifications?]
1899. Kuntze, O. 250 Gattungsnamen aus den Jahren 1737 bis 1763, welche im Kew Index fehlen oder falsch identifiziert sind. Deutsche Bot. Monatsschr. 17: 55–59. 89–91, 107–110. [Seen as unpaged reprint.]
1899. Voss, A. Nomenklatur und Pflanzenkunde. 8 pp.

[Reprinted from Gärtn. Zentral-Bl. 2. Kuntze supporter. Attack on 1735 starting date used by Index Kewensis. English translation by Kuntze 1900.01.]

1900.01 KUNTZE, O. The advantages of 1737 as a starting-point for botanical nomenclature. J. Bot. 38: 7–11. [Translation of Voss's 1899 paper. With J. Britten's editorial "generous" comments on pp. 10–11.]

1900.02.20. KUNTZE, O. Offene Antwort an den Vorstand des Botanischen Vereins der Provinz Brandenburg. 2 pp. San Remo.

1900.02. KUNTZE, O. A plea for my 1737 proposal. J. Bot. 30: 47–50. [With J. Britten's editorial comments on pp. 49–50.]

1900.03? KUNTZE, O. Nomenklaturanfang und Reform internationaler Kongresse. Deutsche Bot. Monatsschr. 18: 33–47. [Reprint seen, 4 pp.]

1900.09? WETTSTEIN, R. VON. Der internationale botanische Congress in Paris und die Regelung der botanischen Nomenclatur. 5 pp. [Reprinted from Oesterr. Bot. Z. 1900 (9): ??–??]

1900.06–09. KUNTZE, O. & T. VON POST. Nomenklatorische Revision höherer Planzengruppen und über einige Tausend Korrekturen zu Englers Phaenogamen-Register. 39 pp. [Reprinted from Allg. Bot. Z. Syst. 1900: 110–120. 1900.06; l.c.: 150–164. 1900.07; l.c.: 179–191. 1900.09. Accepted as Motion 19 In Briquet (1905.03.15: 8).]

1900.08.15. KUNTZE, O. Exposé sur les Congrès pour la Nomenclature Botanique et six Propositions pour le Congrès de Paris en 1900. 15 pp. Genève. [Proposed putting things off until 1905 in Vienna.]

1900.09.28. COOK, O. F. The method of types in botanical nomenclature. Science n.s. 12: 475–481.

1900.12.30. KRAUSE, E. H. L. Reductio generum plantarum. Naturwiss. Wochenschr. 15: 613–614.

1900. PERROT, ÉMILE (SECR.). Actes du I^er^ Congrès International de Botanique tenu a Paris à l'occasion de l'Exposition Universelle de 1900. Lons-le-Saunier.

1900. HALLIER, H. Das prolifierende persönliche und das sachliche, konservative Prioritätsprinzip in der botanischen Nomenklatur. Jahrb. Hamburg. Wiss. Anst. 17: 55–64.

1900. KUNTZE, O. Additions aux Lois de Nomenclature Botanique (Code Parisien de 1867) d'après le Codex Emendatus. 15 pp. [Reprinted from J. Bot. (Morot) 14: .]

1901.03. FERNALD, M. L. Some recent publications and the nomenclatorial principles they represent. Bot. Gaz. (Crawfordsville) 31: 183–197.

1901.11. FERNALD, M. L. The instability of the Rochester Nomenclature. Bot. Gaz. (Crawfordsville) 32: 359–366. [Literature citations.]

1901. BELLI, S. Observations critiques sur la réalité des espèces en nature au point de vue de la systématique des végétaux. [Motion 20 in Briquet (1905.03.15: 8). Not seen.]

1902.03. SHEAR, C. L. Generic nomenclature. Bot. Gaz. (Crawfordsville) 33: 220–229.

1902.04. COOK, O. F. Types and synonyms. Science n.s. 15: 646–656. [Caconyms.]

1902.08.29. ENGLER, A. ET AL. Zusätze zu den Berliner Nomenclatur-Regeln. Bot. Jahrb. 31(Beibl. 70): 24–25. [Additions to the 1897.06 Berlin rules. Accepted as motion 21 in Briquet (1905.03.15: 8).]

1902.12. CLEMENTS, F. E. Greek and Latin in Biological Nomenclature. University [of Nebraska] Studies 3(1): 1–85. [Excellent exposition of classical practices involving word formation, examples, and corrections.]

1902. KRAUSE, E. H. L. Die Autornamen. Allg. Bot. Z. Syst. 7/8: ?–?. [Unpaged reprint of two unnumbered pages: advocated "*Rubus fruticosus* (O. Kuntze Ref. d. Bromb.)."]

1903.05.22. HITCHCOCK, A. S. A note on nomenclature. Science n.s. 17: 827–828. [Objected to a recent case of an author (Scribner) giving preference to an epithet in other than the accepted rank.]

1903.12. POST, T. VON & O. KUNTZE. Lexicon Generum Plantarum. lviii + 714 pp. Stuttgart. [Based on Kuntze's Codex Brevis Maturus, pp. ix–xli, the latter accepted as Motion 22 in Briquet (1905.03.15: 8) and Motion 5 in Briquet (1910.04?: 2).]

1903. BORBÁS, V. Zur Nomenclatur. Magyar Bot. Lapok 2?: ?–?. [2 unnumbered; separate seen in Hungarian and German: concerns author citation of Linnaean binomials with pre-1753 epithet-bringing synonyms.]

1903. MAIDEN, J. H. The principles of botanical nomenclature. Proc. Linn. Soc. New South Wales 27: 683–720. [Excellent survey of then current issues.]

1903. NOLL, F. Vorschlag zu einer praktischen Erweiterung de botanischen Nomenclatur. Bot. Centralbl. 14 (Beihefte): 374–380.

1904.01.15. AMANN, J. ET AL. (Un Groupe de Botanistes Belges et Suisses). Propositions de changements aux lois de la nomenclature botanique. i–iv, 1–45. Georg & Co., Genève, Bâle et Lyon. [Motion 23 in Briquet (1905.03.15: 8).]

1904.03. SACCARDO, P. A. De diagnostica et nomenclatura mycologica. Admonita quedam. Ann. Mycol. 2(2): 195–198. [French (1904.07.31), English (1904.05).]

1904.04. BARNHART, J. H. [Review of Post and Kuntze's] Lexicon Generum Phanerogamarum. Torreya 4: 42–44.

1904.05. CLEMENTS, F. E. Saccardo: De diagnostica et nomenclatura mycologica; admonita quaedam. Translated. J. Mycol. 10: 109–112.

1904.05. ARTHUR, J. C., J. H. BARNHART, N. L. BRITTON, S. BROWN, F. E. CLEMENTS, O. F. COOK, J. M. COULTER, F. V. COVILLE, F. S. EARLE, A. W. EVANS, T. E. HAZEN, A. HOLLICK, M. A. HOWE, F. H. KNOWLTON, G. T. MOROE, E. L. MORRIS, W. A. MURRILL, H. H. RUSBY, C. L. SHEAR, W. TRELEASE, L. M. UNDERWOOD, D. WHITE & W. F. WIGHT (members and alternates of the Nomenclature. Bull. Torrey Bot. Club 31: 249–261 (English); 263–276 (French); 277–290 (German). [Motion 25 in Briquet (1905.03.15: 8).]

1904.05.31. WILLE, N. & V. WITTROCK. Motion au Congrès international de Botanique Deuxième Session. Vienne 1905. Nyt Mag. Naturvidensk. 42: 217–220. [Motion 26 in Briquet (1905.03.15) and Motion 7 in Briquet (1910.04?: 2).]

1904.06.09. AMES, O. ET AL. Propositions de changements aux Lois de Nomenclature botanique de 1867 . . . par les botanistes . . . d'Université Harvard. 32 pp. [French 1–11, English 12–21, German 22–32. Motion 27 in Briquet (1906.07?: 8).]

1904.06.20. HARMS, H. Vorschlag zur Ergänzung "Lois de la nomenclature botanique de 1867," dem in Wien 1905 tagenden Nomenclatur-Kongreß zur Annahme empfohlen. Notizbl. Königl. Bot. Gart. Berlin Appendix 13: 1–37. [Introduced the use of Dalle Torre & Harms numbers for conserved generic names

of flowering plants. Motion 30 in Briquet (1905.03.15: 9).]
1904.06.25. Malinvaud, E. Motion présentée au Congrès international de Botanique de Vienne. 1 [handwritten] page. [Motion 36 în Briquet (1905.03.15: 9).]
1904.06. Saccardo, P. A. Motions supplémentaires présentées au Congrès International de Botanique de Vienne. 1 p. [Motion 35 in Briquet (1905.03.15: 9) and Motion 8 in Briquet (1910.04?: 2).]
1904.06.23. Arcangeli, G. et al. Adjonctions au Code de Paris 1867, proposées par quelques botanistes italiens. 12 pp. [Motion 33 in Briquet (1905.03.15: 9). French pp. 1–3; Italian pp. 5–8; German pp. 9–12.]
1904.06? Additions et modifications aux Lois de la Nomenclature botanique de 1867, approuvées par les membres de la Société de France. 12 pp. [Motion 34 in Briquet (1905.03.15: 9). Not seen.]
1904.06. Rouy, G. Additions et modifications aux Lois de la Nomenclature botanique de 1867. 4 pp. [Motion 37 in Briquet (1905.03.15: 9). Preprinted from longer article (12 pp.) in Rev. Bot. Syst. Géogr. Bot. 2: 1904.07.01.]
1904.06. Saccardo, P. A. Des Diagnoses et de la nomenclature mycologique. Propositions. 6 pp. [French translation by Levier of Saccardo's Latin (1904.06). Preprinted from Boll. Soc. Bot. Ital. 1904: 281–286. 1904.07.31. Motion 28 in Briquet (1905.03.15: 9).]
1904.06. Jaczewski, A. de (rapp.). Projet de la revision des Lois de Nomenclature présenté par la Société Imperiale des Naturalistes de Moscou. 10 pp. Moskva. [Motion 24 in Briquet (1905.03.15: 8) and Motion 6 in Briquet (1910.04?: 2).]
1904.06. Hayek, A. von. Anträge zur Regelung der botanischen Nomenklatur. 10 pp. [Reprinted from Verh. Zool.-Bot. Ges. Wien 54: 341–351. 1904. Motion 32 in Briquet (1905.03.15: 9).]
1904.06. Brunnthaler, J. Motion présentée au Congrès international de Botanique, Vienne 1905. 1 p. [Reprinted from Verh. Zool.-Bot. Ges. Wien 54: 351–353. 1904. Motion 31 in Briquet (1905.03.15: 9).]
1904.06. Carruthers, W. et al. Amendments to the Paris Code of Botanical Nomenclature suggested for consideration of the Vienna Congress of 1905 by the botanists of the British Museum and others. 3 pp. [Motion 29 in Briquet (1905.03.15: 9).]
1904.07. Hochreutiner, G. Observations et propositions présentées au Congrès de Vienne . . . par un groupe de botanistes belges et suisses. 8 pp. [Motion 38 in Briquet (1905.03.15: 9). Not seen.]
1905. Hitchcock, A. S. Nomenclatural type specimens of plant species. Science 21: 828–832.
1905.03.15. Briquet, J. Texte synoptique des documents destinés à servir de base aux débats du Congrès International de Nomenclature Botanique de Vienne 1905. 166 pp. R. Friedländer & Sohn, Berlin.
1905.03.21. Briquet, J. Resumé du travail du Rapporteur général et de la Commission international de nomenclature botanique. 2 pp. Genève. [Outlined what he did since his appointment 17 Nov. 1900.]
1905.05. Pau, C., J. Secall & L. Navás. Observaciones sobre nomenclatura botánica para ser presentadas al 2.° Congreso international de Nomenclatura Botánica de Viena. 13 pp. [Reprinted from Bol. Soc. Aragonesa Ci. Nat. 4: ?.]
1905.12.10. Harms, H. Die Nomenklaturbewegung und der Internationale botanische Kongreß in Wien 1905. Naturwiss. Wochenschr. 20: 785–789.
1905. Schwerin, F. von. Bericht und Betrachtungen über die Resultate des Wiener Nomenklatur-Kongresses. Ber. Deutsch. Dendrol. Ges. 1905: 93–102. [Motion 9 in Briquet (1910.04?: 2). Not seen.]
1905. Hallier, H. Neue Vorschläge zur botanischen Nomenklatur. Jahrb. Hamburg. Wiss. Anst. 22 (Beih. 3); 33–46. [French pp. 43–45; English pp. 45–46.]
1906. Briquet, J. Compte rendu des débats du Congrès international de Nomenclature botanique. Pp. 81–164 and more *in* R. von Wettstein, J. Wiesner & A. Zahlbruckner, Verhandlungen des Internationalen Botanischen Kongresses in Wien 1905.
1906.04.10. Greene, E. L. An unwritten law of nomenclature. Leafl. Bot. Obs. 1: 201–212. [Objected to using personal names as part of generic names. Motion 9 in Briquet (1910:04?: 2).]
1906.08? Briquet, J. (rapp. gén.). Règles internationales de la nomenclature botanique adoptées par le Congrès International de Botanique de Vienne 1905. 99 pp. G. Fischer, Jena.
1906. Nordstedt, O. The starting-point of the nomenclature of Desmids. Bot. Not. 1906: 96–106. [Not seen. Extracted in J. Bot. 45: 128. 1907.03.]
1907.01.28. Otto Kuntze died at 54.
1907.02.04. Schinz, H. & A. Thellung. [On still-born names, pp. 101–102] *in* Begründung vorzunehmender Namesnänderungen an der zweiten Auflage der "Flora der Schweiz" von Schinz und Keller. Bull. Herb. Boissier, ser. 2, 7: 97–112. [Motion 12 in Briquet (1910.04?: 2).]
1907.03. Robinson, B. L. On the rules of botanical nomenclature adopted by the Vienna Congress. Rhodora 9: 30–55.
1907.04. Arthur, J. C., J. H. Barnhart, N. L. Britton, F. Clements, O. F. Cood, F. V. Coville, F. S. Earle, A. W. Evans, T. E. Hazen, A. Hoolick, M. A. Howe, F. H. Knowlton, G. T. Moore, H. H. Rusby, C. L. Shear, L. M. Underwood, D. White & W. F. Wight. American Code of botanical nomenclature. Bull. Torrey Club 34: 167–178. [Motion 11 in Briquet (1910.04?: 2).]
1907.12.10. Schinz, H. & A. Thellung. (Circulaire) du 10 décembre 1907 relative à la question des noms mort-nés. 4 pp. [Motion 13 in Briquet (1910.04?: 2). Not seen.]
1907.12. Rendle, A. B. & J. Britten. Notes on the "List of British seed-plants" II. J. Bot. 45: 433–445. [Still-born names discussion.]
1908.12? Janchen, E. Zur Nomenklatur der Gattungsnamen. Oesterr. Bot. Z. 58(12): 466–470. [Long list to conserve/reject with names and dates only, no citations, no types, no discussion of cases.]
1908. Hayek, A. von. (Sur la question des noms mort-nés). Mitt. Naturwiss. Vereins. Univ. Wien 6: 57–65. [Motion 14 in Briquet (1910.04?: 2). Not seen.]
1909.03.11. Atkinson, G. F. Motions proposant des articles additionels sur la nomenclature des champignons, présentés au IIIme Congrès international de botanique à Bruxelles. 13 pp. Ithaca? [Motion 20 in Briquet (1910.04?: 3). English pp. 9–13.]
1909.06.21. Harms, H. Proposition d'un Index nominum genericorum Pteridophytorum conservandorum, présentée au Congrès international de Botanique de Bruxelles 1910. 3 pp. Berlin. [Motion 35 in Briquet (1910.04?: 4).]

1909.06. RENDLE, A. B. ET AL. Motion proposing an additional clause to the rules of 1905 concerning the nomenclature of algae, suggested for consideration of the Brussels Congress of 1910 by the botanists of the British Museum and others. [Motion 24 in Briquet (1910.04?: 3). Not seen but proposed C. A. Agardh as algal starting point teste TL-2 no. 9067.]

1906.06? POTONIÉ, H. Vorschläge zur Regelung der paläobotanischen Nomenklature. Jahrb. Preuss. Geol. Landesanst 30: 533–537.

1909.07. JANCHEN, E. Proposition d'une Amplification de la List de Noms génériques de Phanérogames, qui doivent être conservés en tous ca. 9 pp. Vienne. [Motion 36 in Briquet (1910.04?: 4).]

1909? DRUCE, G. C. Proposition. 2 pp.? [Replaced six names in the conserved names list. Saw only 1 page.]

1909. SCHINZ, H. & A. THELLUNG. Bericht über eine Enquete betr. die "totgebornen Namen" in der botanischen Nomenklatur. Vierteljahrsschr. Naturf. Ges. Zürich 53: 493–514. [Motion 15 in Briquet (1910.04?: 2). Not seen.]

1909. JANCHEN, E. Zur Frage der totgebornen Namen in der botanischen Nomenklatur. 28 pp. Wien. [Motion 16 in Briquet 1910.04?: 2). Not seen.]

1909. ARTHUR, J. C., E. G. BRITTON, F. E. CLEMENTS, F. S. EARLE & A. W. EVANS. Propositions relatives à l'amendement et au complément des Règles internationales de la Nomenclature botanique, adoptées par les Congrès international de Botanique de Vienne en 1905. 9 pp. [Motion 17 in Briquet (1910.04?: 2).]

1909. RENDLE, A. B. ET AL. Amendments to the international rules for botanical nomenclature, suggested for consideration of the Brussels Congress of 1910 by the botanists of the British Museum and others. 3 pp. London. [Motion 18 in Briquet (1910.04?: 2). Not seen.]

1909. NORDSTEDT, O. Motion au Congrès international de Botanique. Troisième session. Bruxelles 1910. 2 pp. Lund. [Motion 19 in Briquet (1910.04?: 3). Not seen.]

1909. STOCKMAYER, S. Motion au Congrès international de Botanique à Bruxelles 1910, relative à la nomenclature des Algues. 4 pp. Wien. [Motion 21 in Briquet (1910.04?: 3). Not seen.]

1909. SACCARDO, P. A. Da quale anno debba cominciare la validatà della nomenclatura scientifica delle Crittogame. 4 pp. [Motion 22 in Briquet (1910.04?: 3). Reprinted from Ann. Mycol. 7: 339–342. Not seen. Proposed 1753 as starting point for Cryptogams teste TL-2 no. 9946.]

1909. RÖLL, J. Anträge, betr. Aenderungen und Zusätze zu internationalen botanischen Regeln in Bezug auf die Nomenklatur der Sphagna. 12 pp. Darmstadt. 12 pp. [Motion 23 in Briquet 1910:04?: 3). Not seen but see TL-2 no. 9391 for summary.]

1909. STOCKMAYER, S. Motion au Congrès international de Botanique à Bruxelles en 1910, relative à la nomenclature des Cytomorpha 4 pp. Vienne. [Motion 25 in Briquet (1910.04?: 3). Not seen.]

1909. ERIKSSON, J. Comment nommer les formes biologiques des espèces de champignons parasites? Motion présentée au Congrès international de botanique à Bruxelles 1910. Lund. [Motion 26 in Briquet (1910.04?: 3). Not seen.]

1909. FISCHER, E. & P. MAGNUS. Vorschläge zur Nomenklatur der parasitischen Pilze zu Handen des internationalen Kongress von 1910. 1 p. Berne. [Motion 27 in Briquet (1910.04?: 3). Not seen.]

1909. BOTTINI, A. ET AL. Motion proposant un article additionnel aux Règles de 1905 sur la nomenclature des Mousses, présentée par un groupe de bryologues anglais, français et italiens. 1 p. [Motion 28 in Briquet (1910.04?: 3). Not seen.]

1909. DURAND, E.-J. A discussion of some of the principles governing the interpretation of pre-persoonian names, and their bearing on the selection of a starting-point for mycological nomenclature. 13 pp. [Reprinted from Science n.s. 29: 670–676. Not seen. Motion 29 in Briquet (1910.04?: 3).]

1909. NATHORST, A.-G. Motions préliminaires proposant des articles additionnels sur la nomenclature des plantes fossiles présentées au IIIme Congrès international de Botanique à Bruxelles, 14–22 mai 1910. 3 pp. Lund. [Motion 30 in Briquet (1910.04?: 3). Not seen.]

1909. POTONIÉ, H. Propositions pour le règlement de la nomenclature paléobotanique. 7 pp. Berlin. [Motion 31 in Briquet (1910.04.?: 3). Not seen.]

1909. TUZSON, J. Vorschläge zur Regelung de Palaeobotanischen Nomenklatur, zur Beratung auf dem Brüsseler Kongress 1910 vorgeschlagen. 6 pp. Budapest. [Motion 32 in Briquet (1910.04?: 3). Not seen.]

1909. BØRGESEN, F., L. KOLDERUP-ROSENVINGE & O. NORDSTEDT. Motion au Congrès international de Botanique à Bruxelles 1910 (concernant la nomenclature des Chlorophycées, Phaeophycées, et Rhodophycées). 6 pp. Copenhague. [Motion 33 in Briquet (1910.04?: 3). Not seen.]

1909. SCHIFFNER, W. Motion au Congrès international de Botanique à Bruxelles 1910 (concernant la nomenclature des Hépatiques). 4 pp. Vienne. [Motion 34 (Briquet 1910.04?: 4). Not seen.]

1910.04? BRIQUET, J. (SECR.). Recueil des documents destinés à servir de base aux débats de la Section de nomenclature systématique du Congrès International de Nomenclature Botanique de Bruxelles 1910, présenté au nom du Bureau permanent de nomenclature et des Commissions de nomenclature cryptogamique et paléobotanique. 59 pp. [Recognized numbered 36 motions.]

1910.07.22. FARLOW, W. G. & G. F. ATKINSON. The Botanical Congress at Brussels. Science n.s. 32: 104–107. [Also in Bot. Gaz. (Crawfordsville) 50: 220–225. 1910.09.]

1911. COGNIAUX, C. A. Nomenclature horticole. Rapport préliminaire présenté au Congrès international d'Horticulture de Bruxelles (1910). Bull. Soc. Roy. Bot. Belgique 47: 364–424. [First Horticultral Code (pp. 419–424) with 16 Articles, criticized by Briquet as contrary to the Brussels Code just passed (1910) but not yet published (1912).]

1912. BRIQUET, J. (SECR.). Compte rendu des travaux de la Section de nomenclature botanique. Pp. 43–116 (with annexes) *in* É. Wildeman (SECR.), Actes du III^me^ Congrès International de Botanique Bruxelles 1910. Volume 1. Albert de Boeck, Bruxelles.

1912.09? BRIQUET, J. (RAPP. GÉN.). Règles internationales de la nomenclature botanique . . . deuxième Édition mise au point d'après les décisions du Congrès International de Botanique de Bruxelles 1910. 110 pages. G. Fischer, Jena.

1912. Choate, Helen A. The origin and development of the binomial system. Pl. World 15: 257–263.
1914.05. Cook, O. F. Terms relating to generic types. Amer. Naturalist 48: 308–313. [Orthotype, haplotype, logotype, pseudotype, cited usage of monobasic for "monotypic."]
1919.01. Pennell, F. W. Concerning duplicate types. Torreya 19: 13–14. [Credited by J. Ewan (1942.01) with the invention of "isotype" but term used before, see O. F. Cook (1914.05: 309), who cited two previous usages in a different sense.]
1919.04. Hitchcock, A. S. Committee on generic types. Science 49: 333–336. [Rules and recommendations for fixing the types of generic names.]
1921.04. Hitchcock, A. S. Report of the Committee on Nomenclature of the Botanical Society of America. Science 53: 312–314. [The "type-basis" Code.]
1921.05. Hitchcock, A. S. The type concept in systematic botany. Amer. J. Bot. 8: 251–255.
1921.06. Sprague, T. A. Plant nomenclature: some suggestions. J. Bot. 59: 153–160. [Opening of an important discussion: 12 points to change, many examples.]
1921.08. Britten, J. The Vienna Code. J. Bot. 59: 233–234. [Defended legality of Vienna Code recently attacked by N. Britton, Torreya 1919: 244–246. 1919.]
1921.10. Rehder, A. [Letter with more suggestions to Sprague 1921.06.] J. Bot. 59: 289–294.
1921.10. Groves, J. [Comments opposing Sprague 1921.06.] J. Bot. 59: 294–296.
1921.10. Britton, N. L. [Comments opposing Sprague 1921.06.] J. Bot. 59: 296–297.
1921.12. Sprague, T. A. Notes on nomenclature. J. Bot. 59: 345–349. [Important discussion on orthography (*Gluta renghas/benghas* example, latinizing French names ending in -ier and -ière to -erius).]
1922.03. Sprague, T. A. The nomenclature of plant families. J. Bot. 60: 69–73.
1922.04. Hitchcock, A. S. [Suggestions regarding generic names.] J. Bot. 60: 111–112. [Advocating types.]
1922.04. Pennell, F. W. [Comments on plant nomenclature.] J. Bot. 60: 112–118. [Expresses pleasure at Sprague's reopening the subject.]
1922.05. Sprague, T. A. Plant nomenclature: a reply [to Pennell & Hitchcock]. J. Bot. 60: 129–138.
1922.09. Barnhart, J. H. Plant nomenclature. J. Bot. 60: 256–263. [Fascinating commentary on the ongoing discussion.]
1922.07. Wilmott, A. J. Some remarks on nomenclature. J. Bot. 60: 196–201. [Attack on Schinz & Thellung, advocating a "loose" Code.]
1922.09. Barnhart, J. H. Plant nomenclature. J. Bot. 60: 256–263. [Response to Sprague.]
1922.11. Sprague, T. A. [Response to Barnhart.] J. Bot. 60: 313–316.
1922.11. Hitchcock, A. S. [Type-basis code.] J. Bot. 60: 316–318.
1923.01. Fritz, E. A. Plea for common sense in changes of botanical nomenclature. J. Forestry (Washington) 21?: . [Not seen, ref. by Dayton, 1943.05.]
1923.11. Hitchcock, A. S. Type species for the first 100 genera of Linné, Species Plantarum. Amer. J. Bot. 10: 510–514.
1924. Shear, C. L. The failure of the principle of priority to secure uniformity and stability in botanical nomenclature. Science 60: 254–258.
1924.03. Britten, J., J. Ramsbottom, T. A. Sprague (convener), E. M. Wakefield & A. J. Wilmott. Interim report on nomenclature [to Imperial Botanical Conference]. J. Bot. 62: 79–81.
1924.07. Jackson, B. D. History of the compilation of the Index Kewensis. J. Roy. Hort. Soc. 49: 224–229.
1925.04. Green, M. L. Standard species of the Linnean genera of Tetradynamia. Bull. Misc. Inform. 1925: 49–58.
1925. Rendle, A. B. (chairman). Rules of nomenclature. Pp. 300–307 and 384 *in* F. T. Brooks (Secr.), Imperial Botanical Conference London, 7–16 July 1924. Univ. Press, Cambridge.
1925.07. Hanson, H. E. Codes of nomenclature and botanical congresses. Amer. Botanist 31: 114–120. [Summary history.]
1926.03. Sprague, T. A. Standard species. Bull. Misc. Inform. 1926: 96–100. [Residue vs. type method.]
1926.05. Hitchcock, A. S. A basis of agreement on nomenclature. Amer. J. Bot. 13: 291–300. [An important document.]
1926.06.30. Green, M. L. Standard-species of nomina conservanda. 70 pp. Royal Botanic Gardens, Kew. [Distributed softbound 30 June 1926—seen on transmittal note attached to BM copy. Cited reasons for "types" that were omitted in 1929 Proposals of British Botanists. Stafleu (1956.07: 87) noted that this "was circulated among botanists and botanical institutions before and at the Cambridge Congress."]
1927.12. Green, M. L. History of plant nomenclature. Bull. Misc. Inform. 1927: 403–415.
1928.03.I. Suringar, J. V. Personal ideas about the application of the international Rules of Nomenclature, or as with the Rules themselves, international deliberation? Some denominations of I. Coniferous [species.] Meded. Rijks-Herb. 55: 1–76. [Published simultaneously with Part II, Volume 56.]
1923.03.II. Suringar, J. V. Personal ideas about the application of the international Rules of Nomenclature, or as with the Rules themselves, international deliberation? II. Some denominations of dicotyledonous trees and shrubs species. With a retrospection and a set of propositions on the Nomenclature-Rules. Meded. Rijks-Herb. 56: 1–77. [Published simultaneously with Part I, Volume 55. The 30 nomenclature proposals are on 67–75, including submission of names (prop. 24), The Office of Index Kewensis as the standard herbary (prop. 29).]
1929.03.24. Eriksson, J. Question présentée au Congrès International de Botanique à Cambridge (England) 1930. 1 P. Stockholm. [Motion 7 in Briquet (1930.07: iii). Capitalize some species epithets or not.]
1929.03. Mckenzie, K. K. Proposals for modifications of the Vienna-Brussels (so-called International Rules of Nomenclature. 5 pp. (multigr.) New York. [Motion 12 in Briquet (1930.07?: iii). A last gasp in the best style, brief and clear, of the Brittonian school.]
1929.03. Rehder, A. Proposed amendments to the International Rules of Botanical Nomenclature. J. Arnold Arbor. 10: 46–65. [Motion 16 in Briquet (1930.07?: iii). Completed by "16B," A note on names of horticultural variations. J. Arnold Arbor. 10: 66–68.]
1929.06.07. Shear, C. L. Proposed amendments to the International Rules for Botanical Nomenclature. Science 69: 601–602. [Motion 18 in Briquet (1930.07?: iii).]

1929.07.05. GUNDERSON, A. An international list of genera of vascular plants. Science 70: 15–16.

1929.07.22. EWART, A. J. Additional nomina conservanda. 3 pp. (typewritten). Melbourne. [Motion 8 in Briquet (1930.07?: iii). 47 names, mostly species names.]

1920.07. ADAMS, J. Suggested modifications of the International Rules of Botanical Nomenclature. 4 pp. (typewritten). Ottawa. [Motion 1 in Briquet (1930.07: ii).]

1929. DUGGAR, B. M. (EDITOR). Proceedings of the International Congress for Plant Sciences, Ithaca, New York, August 16–23, 1926, Volume 2. George Banta Publishing, Menasha, Wisconsin. [Including:]

1. SPRAGUE, T. A. Principles and problems of plant nomenclature. Pp. 1422–1426.
2. HITCHCOCK, A. S. The relation of nomenclature to taxonomy. Pp. 1434–1439.
3. HITCHCOCK, A. S. (CHAIRMAN). Round-Table discussion: Botanical Nomenclature. Pp. 1556–1570. [Papers by Briquet, Howe, Fernald & Britton.]

1929.08?. BRITISH BOTANISTS. Nomenclature Proposals. 203 pp. London. [The titles in the contents (p. 2) differ from the titles of the works. Motion 5 in Briquet (1930.07?: ii), using titles from contents. Comprises seven works with these titles:]

1. RAMSBOTTOM, J., T. A. SPRAGUE, A. J. WILMOTT & E. M. WAKEFIELD [Britten died 1924.]. Proposals by the sub-committee on nomenclature, appointed by the Imperial Botanical Conference, London, 1924. Pp. 3–45. [See Rendle (1925).]
2. SPRAGUE, T. A. Proposal for the conservation of 90 additional generic names. Pp. 46–96.
3. GREEN, M. L. Proposed standard-species of Nomina Generica Conservanda. Pp. 97–109. [This is a truncation of the original (Green, 1926.06.30), now omitting the stated reason for each choice.]
4. HITCHCOCK, A. S. & M. L. GREEN. Standard-species of Linnean genera of Phanerogamae (1753–1754). Pp. 110–199.
5. WAKEFIELD, E. M. Proposals. P. 200.
6. WILMOTT, A. J. Proposal. Pp. 201–202.
7. BURKILL, I. H. Proposal. P. 203.

1929. CIFERII, R. Proposte di modificazioni alle Regole di Nomenclatura Botanica. 1 p. [Motion 2 in Briquet (1930.07?: ii).

1929. ARTHUR, J. C. Proposed amendments to the International Rules of Botanical Nomenclature. 4 pp. [Page 1 is reset from J. Bot. 67: 258–259. 1929.09 Motion 3[A] in Briquet (1930.07?: ii). Pp. 2–4 Motion 3[B] is typed.]

1929. AUDAS, J. W. ET AL. Nomina conservanda. 3 pp. (typewritten). [Motion 4 in Briquet (1930.07?: ii). The Committee on Australian Botanical Nomenclature was "appointed at a meeting of the Australasian Association for the Advancement of Science in 1924."]

1929. SEWARD, A. C. ET AL. [Memorandum.] 1 p. (typewritten). [Motion 6 in Briquet (1930.07?: iii). Foresters and botanists favoring species conservation and a judiciary to solve questions of nomenclature.]

1929. FERNALD, M. L. & C. A. WEATHERBY. Proposed amendments to the International Rules of Botanical Nomenclature. 6 pp. Boston. [Motion 9 in Briquet (1930.07?: iii). Not seen.]

1929. GUNDERSON, A. Proposed amendments to the International Rules of Nomenclature. 2 pp. (typewritten). Brooklyn. [Motion 10 in Briquet (1930.07?: iii). Completed by: "10A" An international list of genera of vascular plants. Science 70: 15–16. 1929.07.05, and "10B" Genera Pteridophytorum et Spermatophytorum Variationes Nomenclaturae. 13 pp. (typewritten) and dated March 1929.]

1929. HITCHCOCK, A. S. Proposed amendments to the International Rules of Botanical Nomenclature. 3 pp. (multigr.). Washington. [Motion 11 in Briquet (1930.07?: iii).

1929. OLIVER, W. R. B. Additional articles and amendments to the International Rules of Botanical Nomenclature. 2 pp. Wellington, New Zealand. [Motion 13 in Briquet (1930.07?: iii).]

1929. PENNELL, F. W. Some proposals for modification of the "International Rules of Botanical Nomenclature." 1 p. (typewritten). Philadelphia. [Motion 14 in Briquet (1930.07?: iii).]

1929. PFEIFFER, H. Ueber 70 neue Namencombinationen in einer einzigen Cyperaceengattung oder Aufnahme eines Gattungsnamens in den Index der "Nomina conservanda?" 7 pp. Berlin. [Motion 15 in Briquet (1930.07?: iii).]

1929. SHEAR, C. L. Proposed additions to the list of Nomina conservanda of the Rules for Botanical Nomenclature. 1 p. (typewritten). Washington. [Motion 17 in Briquet (1930.07?: iii).]

1929. SURINGAR, J. V. Propositions on the International Rules of Botanical Nomenclature in regard to the International Botanical Congress in London. 1930. 27 pp. Wageningen. [Motion 19 in Briquet (1930.07?: iii). Completed by "19A" Supplementary remarks. 1 p. Wageningen and "19B" Literature to be added in Appendix of propositions on the Intern. Rules of Bot. Nomenclature (London Congress 1930). 1 p. Wageningen. 60 species names for conservation.]

1929. WHERRY, E. T. A plea for the conservation of *Shortia* as a generic name. 2 pp. (typewritten). Washington. [Motion 20 in Briquet (1930.07?: iv).

1929. SURINGAR, J. V. The American Code, The Vienna Code and the resolutions of the Imperial Botanical Conference in London. Will agreement be possible in 1930? Meded. Rijks-Herb. 57: 1–[43].

1930.07? BRIQUET, J. (RAPP. GÉN.). Recueil synoptique des documents destinés à servir de base aux débats de la sous-section de nomenclature du V^me^ Congrès International de Botanique Cambridge (Angleterre) 1930. 142 pp. R. Friedländer & Sohn, Berlin.

1930.08. BRIQUET, J. (RAPP. GÉN.). Avis préalable du Bureau Permanent des Commissions de nomenclature sur les motions soumises aux débats de la sous-section de nomenclature du V^me^ Congrès International de Botanique Cambridge (Angleterre) 1930. 25 pp. R. Friedländer & Sohn, Berlin.

1931.07. GREEN, M. L. Rules of botanical nomenclature . . . . Empire Forest. J. 10(1): 54–72.

1931. BRIQUET, J. Compte rendu des débats de la sous-section de nomenclature botanique. Pp. 554–654 *in* F. T. Brooks & T. F. Chipp, Report of the Proceedings [of the] Fifth International Botanical Congress Cambridge, 16–23 August 1930. University Press, Cambridge.

1931.10.26. John Isaac Briquet died at 62.

1932.03. MOLDENKE, H. N. A discussion of tautonyms. Bull. Torrey Bot. Club 59: 139–156. [Updated Huth.]

1933. SPRAGUE, T. A. Plant nomenclature. Bot. Soc. Exch. Club Brit. Isles 1932: 300–313. [Chief pro-

visions as amended illustrated by examples from British flora.]
1933.11. FRIZZELL, D. L. Terminology of types. Amer. Midl. Naturalist 14: 673–668. [Alphabetic listing of 233 kinds of types with usage references.]
1934.06. RENDLE, A. B. International Rules of Botanical Nomenclature adopted by the Fifth International Botanical Congress, Cambridge, 1930. J. Bot. 72(Suppl.): 1–29.
1934.10. MOLDENKE, H. N. A supplementary list of tautonyms and miscellaneous nomenclatural notes. Torreya 34: 5–10.
1934.12.12. DODGE, C. W. Proposals for amendment of Art. 20 of the International Rules of Nomenclature. Ann. Missouri Bot. Gard. 21: 709–712. [Proposal 9 in Sprague 1935.07: 2).]
1934.12. SAMPAIO, A. J. DE. La méthode de types et la nomenclature analogique. Ann. Acad. Brasil. Sci. 6(4); 173–179. [Proposal 13 in Sprague 1935.07: 2). Series of examples formed in accordance with Rec. X & XI.). Not seen.]
1934. ADAMS, J. Some amendments to the International Rules of Botanical Nomenclature. 8 pp. (typewritten). Ottawa. [Proposal 1 in Sprague (1935.07: 1). Not seen.]
1934. HOCHREUTINER, B. P. G. Proposals for the modification of Art. 35, Rec. xxx, and Art. 72. Remarks concerning Art. 38. 2 pp. (typewritten). Genève. [Proposal 10 in Sprague (1935.07: 2). Not seen.]
1934. REHDER, A. Amendments to the International Rules of Nomenclature, 3rd edition. 4 pp. Arnold Arboretum. [Proposal 12 in Sprague (1935.07: 2). Not seen.]
1935? ARTHUR, J. C. Proposed amendments to the International Rules of Nomenclature. 1 p. Lafayette. [Proposal 2 in Sprague (1935.07: 1). Not seen.]
1935? AUSTRALIAN BOTANISTS. Motion for conservation of the generic name *Haussmannia* . . . four specific names . . . . 1 p. (typewritten). [Proposal 3 in Sprague (1935.07: 1). Not seen.]
1935. BECHERER, A. Vorschläge fur die Nomenklatur-Kommission des Botaniker Kongresses in Amsterdam. 3 pp. (typewritten). Genf. [Proposal 4 in Sprague (1935.07: 2). Not seen.]
1935. DANSER, B. H. Proposals concerning the formation, spelling and gender of botanical names. 3 pp. (typewritten). [Proposal 7 in Sprague (1935.07: 2). See also Danser, 1935.04).]
1935. DIXON, H. N. Proposals concerning bryological nomenclature. Rev. Bryol. Lichénol. 7: 137–141. [Proposal 8 in Sprague (1935.07: 2). Not seen.]
1935. TROUP, R. Motions submitted on behalf of various Forestry Institutions and Societies. 3 pp. Oxford: [Proposal 14 in Sprague (1935.07: 3). Not seen.]
1935.01. JONGMANS, W., T. G. HALLE & W. GOTHAN. Proposed additions to the International Rules of Botanical Nomenclature. 15 pp. Haarlem. [Proposal 11 in Sprague (1935.07: 2). Not seen.]
1935.02. "Briquet, J." (deceased). International Rules of Botanical Nomenclature . . . revised by the International Botanical Congress of Cambridge, 1930 [as] compiled by the Editorial Committee for Nomenclature from the Report of the Subsection of Nomenclature prepared by John Briquet (deceased). 152 pp. G. Fischer, Jena. [English by A. B. Rendle, French by B. P. G. Hochreutiner, German by H. Harms.]
1935.03. SPRAGUE, T. A. (EDITOR). [12 botanists'] Additions and amendments to the International Rules of Botanical Nomenclature, 3rd edition. Bull. Misc. Inform. 1935: 65–92. [Proposal 5 in Sprague (1935: 07: 2).]
1935.04.11. LOOSER, G. Motion pour déclarer "nomen conservandum" le genre *Cryptocarya* R. Br. et "nomen rejiciendum" le genre *Peumus* Mol. (Lauraceae). 1 p. (typewritten). Santiago, Chile. [Proposal 17 in Sprague (1935.09.01: 3). Not seen.]
1935.04. DANSER, B. H. Grammatical objections to the International Rules of Botanical Nomenclature, adopted at Cambridge in 1930. Blumea 1: 295–304. [Proposal 15 in Sprague (1935.09.01: 2). Orthography—"leave this question to a committee of botanists who are more or less competent . . ."; see Sprague rebuttal (1935.08).]
1935.04. MOLDENKE, H. N. Additional notes on tautonyms. Bull. Torrey Bot. Club 59: 139–156.
1935.04. SPRAGUE, T. A. Survey of nomenclature (1930–1935). Chron. Bot. 1: 34–35.
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1939.05. ALM, C. G. ET AL. Amendment of Art. 68. 1 p. Göteborg. [Proposal 1940–3 in Lanjouw (1950.04?: xiii).]

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1. SPRAGUE, M. L. (M. L. GREEN). The case for the botanists. 126–134.
2. HEMMING, F. The case for the zoologists. Pp. 134–137.
3. WILMOTT, A. J. A criticism. Pp. 138–140.
4. TREWAVAS, E. Comments. Pp. 141.
5. SPRAGUE, T. A. Comments. Pp. 141–142.
6. NEAVE, S. Comments. p. 142.
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1946.07. BAILEY, L. H. Species names with capital letters [and] observations on binomials. Gentes Herbarum 7: 168–174. [For capitalizing, explains that the comma between binomial and author means "of," opposes infraspecific names.]

1947.04.01. CAMP, W. H., H. W. RICKETT & C. A. WEATHERBY. International Rules of Botanical Nomenclature . . . revised by the International Congress of Amsterdam, 1935. Brittonia 6: 1–120. [The Brittonia Code.]

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1948.04. LITTLE, E. L. A proposal to stabilize plant names. Phytologia 2: 451–456. [Nomen extinctum—unused for 100 years, upping the ante from the Berlin code (1897.06) of unused for 50 years.]

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1948.07.15. MERRILL, E. D. Nomenclatural notes on Rafinesque's published papers 1804–1840. J. Arnold Arbor. 29: 202–214. [Proposal 1950–3 in Lanjouw (1950.04?: xvi).]

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1949.01. SHERFF, E. E. (CHAIRMAN). Symposium on botanical nomenclature. Amer. J. Bot. 36: 1–32. Comprising:

1. SHERFF, E. E. Introduction. Pp. 1–4.
2. WEATHERBY, C. A. Botanical Nomenclature since 1867. Pp. 5–7.
3. BLAKE, S. F. Byways of nomenclature. Pp. 8–9. [Linnaeus, Rafinesque, Saint-Lager, Bubani.]
4. RICKETT, H. W. An editor's point of view. Pp. 10–13.
5. MERRILL, E. D. Adventures in locating validly published but unlisted binomials. Pp. 14–19.
6. PENNELL, F. W. Toward a simple and clear nomenclature. Pp. 19–22.
7. BAILEY, L. H. Problems in taxonomy. Pp. 22–24.
8. ROSEDAHL, C. O. The problem of subspecific categories. Pp. 24–27.
9. JUST, T. The nomenclature of fossil plants. Pp. 28–32.

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1949. TROUPIN, G. La terminologie des types en botanique systematique. Bull. Soc. Roy. Bot. Belg. 82: 57–66.

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1950.05. POLUNIN, N. Specific and trivial decapitalization. Bull. Torrey Bot. Club 77: 214–221. [Important statement pro decapitalization.]

1950.06. HJELMQVIST, H. The conservation of species names [invited responses]. Bot. Not. 1950: 328–347.

1. RICKETT, H. W. Pp. 328–329. [Opposed.]
2. GRAM, K. Pp. 330–332. [Pro, needed for stability.]
3. CAMP, W. H. Pp. 332–336. [Unrealistic without staff.]
4. JANCHEN, E. Pp. 336–340. [Yes but must be limited.]
5. GILMOUR, J. S. L. Pp. 341–343. [Yes but must be limited.]
6. BAEHNI, C. Pp. 343–346. [Conservation of species = sea serpent.]
7. SKOTTSBERG, C. Pp. 346–347. [Fix the rules then no name changes.]

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1950.07.18. International Association for Plant Taxonomy born by resolution of the Stockholm Congress.

1950.08? LANJOUW, J. (EDITOR). Botanical nomenclature and taxonomy, a symposium organized by the International Union of Biological Sciences with support of UNESCO at Utrecht, the Netherlands, June 14–19, 1948. Chron. Bot. 12(1/2): 1–87. comprising:
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3. INTERNATIONAL COMMISSION FOR NOMENCLATURE. Pp. 59–62.
4. SPRAGUE, T. A. International Rules of Botanical Nomenclature Supplement embodying the alterations made at the Sixth International Botanical Congress, Amsterdam, 1935. Pp. 65–77; Appendix II, pp. 79–80; Appendix III, pp. 81–83; Index of plant names, pp. 85–87.

1950.11. WIT, H. C. D. DE. Changes in the International Rules of Botanical Nomenclature made by the 7th Int. Bot. Congress at Stockholm. An unofficial review. Fl. Males Bull. 1(7): 197–231.

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1953.09. RICKETT, H. W. Expediency vs. priority in nomenclature. Taxon 2: 117–124. [Historical survey with bibliogaphy.]

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1954.04. STAFLEU, F. A. Report [on] The Genève Conference on botanical nomenclature and Genera Plantarum organized by the Botanical Section of the International Union of Biological Sciences 25–30 January 1954. Regnum Veg. 5: 1–59.

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1954.09. [STAFLEU, F. A.] [Decisions taken at] VIIIth International Botanical Congress, Paris, 1954, Nomenclature Section. Taxon 3: 184–196.

1954.11. STAFLEU, F. A. Nomenclature at the Paris Congress. Taxon 3: 217–225.

1955.08. STAFLEU, F. A. Huitième Congrès International de Botanique, Section Nomenclature. Taxon 4: 121–177.

1956.07. STAFLEU, F. A. Nomenclatural conservation in the phanerogams. Taxon 5: 85–95. [Historical review about conserved generic names.]

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1960.12. LANJOUW, J. IXth International Botanical Congress, Nomenclature Section, report presented by the Bureau of Nomenclature. Regnum Veg. 20: 1–116. Reprinted from Proc. IX Int. Bot. Congr. Montreal 1959 3: 27–116.

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1961.12. LANJOUW, J. ET AL. (EDITORS). International Code of Botanical Nomenclature adopted by the Ninth International Botanical Congress, Montreal, August 1959. Regnum Veg. 23: 1–372.

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1964.04. HELLER, J. L. The early history of botanical nomenclature. *Huntia* 1: 33–70. [Linnaean period: credited Linnaeus for inventing trivial names [epithets] that led, after his death, to binomial nomenclature. Attributed invention to Linnaeus's struggle to reform book citation.]

1964.06. [STAFLEU, F. A.?] Nomenclature proposals Xth Congress: preliminary vote. Taxon 13: 183–187.

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1966.11. STAFLEU, F. A. Tenth International Botanical Congress, Edinburgh, 1964: Nomenclature Section [proceedings.] Regnum Veg. 44: 1–75.

1966.12. LANJOUW, J. ET AL. (EDITORS). International Code of Botanical Nomenclature adopted by the Tenth International Botanical Congress Edinburgh, August 1964. Regnum Veg. 46: 1–402.

1967.11. DANDY, J. E. Index of generic names of vascular plants 1753–1774. Regnum Veg. 51: 1–130.

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1970.02. MOORE, H. E., F. A. STAFLEU & E. G. VOSS. XI International Botanical Congress: final mail vote and Congress action on nomenclature proposals. Taxon 19: 43–51.

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1972.03. STAFLEU, F. A. (CHAIRMAN) & E. G. VOSS (SECR.). International Code of Botanical Nomenclature adopted by the Eleventh International Botanical Congress Seattle, August 1969. Regnum Veg. 82: 1–426.

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1979.12? VOSS, E. G. Section 1. Nomenclature. Pp. 129–186 *in* D. V. Lebedev et al. (editors), Proceedings, XII International Botanical Congress, Leningrad, 3–10 July 1975. Leningrad, Nauka.

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1983.10. VOSS, E. G. (RAPP. GÉN.) & W. GREUTER (VICE-RAPP.). International Code of Botanical Nomenclature adopted by the Thirteenth International Botanical Congress, Sydney, August 1981. Regnum Veg. 111: 1–472.

1987.02. GREUTER, W. (RAPP. GÉN.) & J. MCNEILL (VICE-RAPP.). Synopsis of proposals on botanical nomenclature, Berlin, 1987. Taxon 36: 174–281. [334 proposals.]

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WHO CONQUERED THE NEW WORLD? OR FOUR CENTURIES OF EXPLORATION IN AN INDEHISCENT CAPSULE

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ABSTRACT

We track botanical conquest from Oviedo (who met Columbus in 1490 and visited Santa Marta, present Colombia, in 1515) to the corporate botanical garden at the close of the 19th century. We also recognize the foreign correspondent of the 16th century; the solitary missionary-naturalist of the 17th century; the apologist of systems (who advocates schemes of classification) in the 18th century; and the naturalist-collector, then often a member of a government-sponsored expedition in the 19th century.

History? We are making history. Plant taxonomy is not a purely descriptive science, it is history, deviously directed toward a conclusion. History rests on archives of two sorts: books published from archives, and plant mummies ticketed or labeled and entombed in herbaria. The conquest of the New World by the explorers who observed and reported begins with Columbus who met Oviedo two years before Columbus set sail. We headline the sixteenth century for its commentators on the plants observed; the seventeenth century by the missionaries who collected seeds and, now and then, specimens; the eighteenth century by apologists of systems, collecting exhibits to support their schemes; the nineteenth century by the field collector-explorer who filled, not cabinets of curiosities, but museums which by the twentieth century would overflow.

Floras, faunas, history, everything flows, *omnia fleurit*. When did the sea bean, *Entada gigas*, first take the Gulf Stream across the Atlantic? The soft pithlike wood of *cuipo* or quipo (*Cavanillesia platanifolia*), a relative of *ceiba*, for centuries had been washed on the Azores by tempests. Indeed, these waifs were gathering evidence for what in Columbus's day was still looked upon as shoreless seas.[2] When he was coasting among the Bahamas on the first of his four voyages, Columbus wrote: "I believe there are many plants and many trees which are worth a lot in Spain for dyes, and for medicines and spicery; but I do not recognize them, which gives me great grief."[3] Pineapple as a domesticate from the Mosquito Coast was described, for example, by Columbus's son Ferdinand as a "great pine cone; and the plant is grown in large fields [in Veragua, Panama] from shoots that grow out of the same piña [and] plants last for three or four years, always producing fruit."[4] (See Fig. 1.)

Pineapple was transplanted by Guaranies of south Brazil and Paraguay—the word *Ananas* is a Tupi-Guarani name—via other Amerindians probably down the Orinoco avenue of penetration to the Caribbean. The Portuguese had delivered it as far as Goa on the Indian Ocean during the sixteenth century. But pineapple was not the staple food that maize was, "the most important of all foods for men and their livestock."[5] By the late sixteenth century the peoples of central Africa were raising maize, manioc, peanuts, and squashes, all American domesticates, but we do not know exactly who those phyto-conquestadors were, who delivered the foodstuffs, or how early they arrived. So disproportionate was the west-to-east movement that Vavilov listed 640 New World plant domesticates but only 50 of African origins.[6]

Weeds from tropical or warmer climates had arrived in the Mediterranean from even before the days of Marco Polo, and these Old World emigrants arrived in Hispaniola in 1494 on the 17 ships of Columbus's second voyage. (Do you remember the *Santa María*, *Pinta*, and *Niña* from your schoolbook history days? The *Niña* returned to Hispaniola in 1494.) On board were 1,200 men (no women) taken abroad to build the settlement near Isabela.[7] Imagine the weed seeds that arrived when rootcrowns of the grape vines and sugar cane from Spain and her possessions were planted.

Bixa, the body paint of jungle Indians, in mod-

[1] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

FIGURE 1. Pineapple grown and illustrated in 1697 at the botanic garden in Amsterdam. This drawing served as a basionym in the description of the pineapple by Linnaeus in the *Species Plantarum* in 1753.

ern times has been sublimated into coloring for cheese and margarine. In 1526 Oviedo said the Caribs "paint their bodies [and] make themselves hideous [with] various figures on their faces and other parts of the body [thinking] they look good in it, and besides they like the appearance of the paint.[8] Gaspard Bauhin cited Oviedo, and from the dehiscent capsule of *annatto* placed it in the generic group, *Castanea*.[9] When Linnaeus named *Bixa orellana* he commemorated Francisco Orellana, taking his flag from Plukenet who had pictured *Bixa* by its other name *achiote*.[10] Alexander Smith, employed in the Economic Museum at Kew, contributed to the *Treasury of Botany* of Lindley and Moore. Smith wrote that *Bixa* paint [was] almost their only article of clothing.[11] Perhaps *Bixa* gave the designation "Red Man."

Tidings were circulated in Pizarro's time that a sort of cinnamon grew on the east slope of the northern Andes. "The Land of Cinnamon" was placed as east of Quito, and Orellana was dispatched to accompany Francisco Pizarro's brother Gonzalo on an expedition to a province called *Quijos* to find this "*Canella alba*" or "*Ispingo*." Gonzalo Pizarro chronicled that when they were "on the skirts of a volcano," evidently *Cayambe*, it did not cease to rain for a single day for two months. He said the Spanish "received great injury, and much of their clothing became rotten." In the vicinity of Sumaco the Indians went naked, Pizarro concluding, "they go naked because the country is so hot, and it rains so much that clothes become rotten."[12] No specimens from this Spanish Pizarro period exist. It was probably Joseph de Jussieu who in 1747 first collected a sterile specimen that Lamarck labeled *Laurus quixos* and preserved in the Paris herbarium.[12a] Here at the Missouri Botanical Garden, Henk van de Werff is piecing together this complex history four centuries after Pizarro.

Although Santa Catalina Island was discovered off the southern California coast in October 1542 by Cabrillo, there was no botanist aboard the *San Salvador* or its consort, *La Victoria*, and it was 300 years before William Gambel botanized on the island in 1847.[13] The University of Padua, not Cabrillo's Spain, opened the first botanic garden in Europe nearly a half century after Columbus.[14] The next botanic gardens, Leyden (1590) and Montepellier (1592), featured materia medica exhibits or plants involved in the economy of the nation. American plants were grown at Oxford, which opened its garden in 1621, Paris in 1635, and Uppsala in 1655. The great surge of living collections advanced with Kew in 1759 and her 13 satellite gardens throughout the far-flung British Empire. In due course there was a particular one outside the British crown—Shaw's Garden, created in the image of Kew.

The growth of botany, systematic botany in particular, depends on the comparative forms of flowers afforded in a botanic garden. Just as vegetation types are mapped by so-called indicator species, botanic gardens stake the growth of horticulture and advance taxonomy. Notable are the Chinese studies nurtured by Arnold Arboretum's Chinese plantings.

We recall that Mexico City and Lima opened universities in 1553 and 1555, and that the New World's first herbal, though not published for four centuries, dates from 1552. It is the *Badianus Manuscript*.[15] This Aztec herbal records such modern concepts as the relation of hummingbirds to the tubular scarlet flowers of, for example, *Loeselia coccinea* (Polemoniaceae). There are puzzles: the aroid *huacalxochitel*, meaning "basket flower," was illustrated for its value in curing angina. Tom Croat tells me it is "presumably a fanciful rendition

of some *Philodendron*." The tendrils in the drawing are unnatural; a few aroids do have lobed leaves, but none has blades close to those pictured. Many narrow-endemic philodendrons occur in Mexico, and so, in twentieth century thinking, "perhaps it represents an extinct species." Among other engaging illustrations in the *Badianus Manuscript* are the very earliest illustrations of American cacti, a cereoid and an opuntia.[16] Remarkably this 1552 herbal offers notes on Old World immigrants: *Rumex*, *Oxalis*, and *Cynara cardunculus*. Early records of New World *Parthenium hysterophorus*, and such fruits as mombin (*Spondias purpurea* L.) are in this Mexican herbal.

The Franciscan friar André Thevet was on the coast of Brazil in November 1555.[17] Later he sailed along the Florida coast and reached the Gulf of St. Lawrence. Thevet's Canadian journal was cited by Linnaeus in his *Bibliotheca botanica* (1747), where it was the first of what Linnaeus listed as "*peregrinationes Americani*." Thevet antedated Jacob Cornut's Canadian account by 78 years, but Cornut offered about 30 plant descriptions. The indehiscent capsules of the attractive genus *Thevetia* bring him to mind. (The *Flora of Panama* describes these distinctive fruits as "drupes.")[18] A century before Linnaeus[19] "Ahovay" was included by Gaspard Bauhin in his *Pinax* under "Pomiferae Arbores" together with genipat and durion. Under a six-word polynomial Bauhin cited Jean de Lery, Protestant pastor who visited Brazil the year after Thevet, and who noted the fruit of Ahovay (*Thevetia*) as a *crepitaculum*, Latin for rattle. Domestic uses of plants are the first chronicled by the sixteenth century herbalists Clusius and L'Obel. The Tupinambas of Brazil wore *Thevetia* "shells" as anklets in their dances. When the barber-surgeon John Gerard produced his *Herball* or *Generall Historie of Plantes* for British readers, the year Shakespeare's "Henry the IV" was on the stage, Gerard figured a woodcut of *Thevetia*, the "Indian Morrice bells," in an allusion to the exotic Morocco dance theme. He said their "rattling sound doth much delight" the Indians.[20]

Only one of the several herbalists of the sixteenth century included American discoveries, so slow was the spread of plant lore. Brunfels included no American headlines, not even holy wood, *Guaiacum officinale* or *sanctum*, the prized antisphyilitic, which by 1530 was selling briskly. Fuchs alone of the herbalists illustrated two New World squashes and maize.[21] By 1583 Clusius of Antwerp, who profited from his residence in a port city on the North Sea, mentioned the "White beans of Guatemala" and "dama de noche."[22]

FIGURE 2. Pepper Tree of Chile illustrated by Feuillee in 1714, introduced into California during the Mission Period.

Before we leave the foreign correspondents of the sixteenth century, a word about Old World preconceptions that have left us with some everyday misnomers. For centuries maize was known as Turkey wheat, the American bison is still called buffalo, and the (spotted) jaguar, the Tupi Guarani name, has prestigious advertising value, nevertheless, the Old World association, *el tigre*, is the popular Latin American name today. When the American agave was named it became the "American aloe." David Quinn called these "products of wishful thinking."[23] The Greek word for a spiny plant is *kaktos*, appropriated for the cactus. John Lindley knew our avocado as Alligator pear, "pear" going back to Oviedo from its shape.[24]

Who were the solitary missionary-naturalists of the seventeenth century? First let us mention John Banister of the York River region of Virginia.[25] Had the Reverend Banister lived beyond his 38 years, North American natural history would have taken a very different course indeed. Banister took his M.A. degree at Oxford in 1674 and became clerk and chaplain at Magdalene College. He studied and collected especially the surviving plants brought back from the York River area that had

earlier been noticed by John Tradescant between 1632 and 1654. From 1678 to 1692, when Banister was accidentally shot while collecting on the Roanoke River, two-thirds to three-quarters of the plants described by Banister from Virginia were new. Leonard Plukenet had 89 of Banister's drawings finely engraved and reproduced in his *Phytographia*, with the Latin descriptions. However, he failed to credit Banister with 11 of these, mostly those received in England after Banister's death. Plukenet's Banister records were an important contribution to the writings of Linnaeus 50 years later. When Linnaeus quoted Gronovius or the works of Ray, Morison, Plukenet, Petiver, and Dillenius for records of Virginia plants, he was quoting Banister and was basing his newly described species on one of Banister's drawings or descriptions, although Linnaeus rarely attributed these to him. The monk Louis Feuillée (1660–1732) explored Martinique, Caracas, and elsewhere before visiting the coasts of Chile and Peru between 1707 and 1712, observing especially the ports of Concepción, Talcahuano, Coquimbo, and Callao. Linnaeus cited plants from the illustrated journal of Feuillée, but no specimens are known. The pepper tree, so well known in southern California, was cited from Feuillée as *Schinus molle* where the trivial epithet is without meaning, a mistake for *mulli*, the native vernacular name in Chile.[26] (See Fig. 2.)

The Catholic missionary Charles Plumier (1646–1704) visited Martinique and Haiti in 1689 with Joseph Donat Surian, physician-pharmacist.[27] Surian returned to France the next year with a plant collection, which is preserved in ten books in the natural history museum in Paris. Instead of collecting plants Plumier made about 6,000 line drawings and prepared early descriptions of the plants observed. These were the bases of four botanical works published between 1693 and 1760. They were completed by Johannes Burman who wrote the later descriptions.

The eighteenth century may be marked by the advocates or apologists for the two historic systems of plant classification launched in that century. The Sexual System espoused by Linnaeus, and its impact, has been skillfully told by Frans Stafleu in his *Linnaeus and the Linnaeans* (1971), with some references to the succeeding scheme, the emerging Natural System of Jussieu. I summarized in my "Plant Collectors in America: Backgrounds for Linnaeus" in 1970,[28] but we await a capsulated review of the American collectors and sources that contributed to Jussieu's natural arrangement.

Linnaeus is well known for his *Systema Naturae* published in 1735. The same year a clockmaker in England, John Harrison, invented the first chronometer to enable ships to determine longitude at sea. The use of the chronometer was opposed by the astronomer royal, Nevil Maskelyne, and so it was not used on the *Endeavour* by Captain Cook. It became crucial in later voyages.[29] The chronometer and the sextant enabled expeditions to reach and to map charted shores accurately. The harvest of those expeditions would still be sorted by the numbers of their stamens and pistils into new genera and species according to Linnaean classes.

The description and classification of new plants in the New World followed in the wake of such applied botanical activities as the culturing of silkworms on leaves of mulberry trees. The founding of the Colony of Georgia is said to have rested on three needs: an asylum for debtors and persecuted Protestants; a trial garden for the growing of silk, wine grapes, and drug plants; and a relief of population pressures in the Old World.[30] Old Ebenezer, a sterile and unattractive spot about 21 miles from Savannah and about four miles below the present town of Springfield, Effingham County, was settled in the spring of 1734 by 78 Salzbergers. George Genzmer described them as "simple folk, pious, industrious, uneducated, impoverished by confiscation and exile, and bewildered by their situation on the Georgia frontier." Baron von Reck and Reverend Johann Bolzius led a "tour of observation into the adjoining country [to Savannah] sponsored by Governor Oglethorpe.[31] Old Ebenezer had proved unsatisfactory—in 1736 the settlers moved to a high ridge and founded New Ebenezer. Central to my mentioning Ebenezer is the appearance in 1756 of an almost entirely overlooked botanical paper published in *Hamburgisches Magazin* enumerating 87 plants, mostly economic or potentially useful species: the report of the Reverend Bolzius.[32]

Dr. William Houstoun botanized in the West Indies, Vera Cruz, and the Spanish Main on behalf of Sir Hans Sloane and the Chelsea Physick Garden.[33] His premature death in Jamaica, August 14, 1733, brought an end to the plan of Oglethorpe and the South Sea Company, by whom Houstoun was retained as a physician, for shipping plants and seeds from tropical America to West Indian ports, to Charleston, and to the "Colony of Georgia in America." Some West Indian plants reached the Savannah plantations from Houstoun's travels.[34] His energies in other regions and the many new species he discovered and made known by Philip Miller indicate that the history of Georgia botany would have been very different had he lived.

Men of the nineteenth century at watersheds around the world who directed the flow of knowl-

edge from explorations included Barton, Humboldt, the Hookers, the de Candolles, Martius, Engler, Torrey, and Gray. Humboldt's enquiry into many fields is "unlikely ever to be surpassed, for thoroughness, perseverance, curiosity, courage, and sheer force of intellect."[35] Humboldt's was the last moment in history when an individual could master all branches of science. William Jackson Hooker, as did S. F. Baird in this country, implemented the field naturalists, often out of their own pockets, to assemble at Kew the records of global exploration. Witness, for example, that George Gardner, M.D., aided by Hooker, from 1836 to 1841 wrote 36 letters, some 18 and 24 pages long. Gardner's comments in his Brazilian *Travels* (1846) are often to the point: the Rio botanic garden, Gardner wrote, is "more a promenade than a Botanic Garden."[36] Joseph Dalton Hooker, who cultivated Kew after his father's seeding, saw the international values of colonial floras, still of first-line usefulness, for the West Indies, Hongkong, British India, and so forth. The elder de Candolle, Augustus Pyramus de Candolle, first used "endemique" in 1820.[37] His *Prodromus*, published from 1823 to 1873, with his son, Alphonse, involved British and continental authors. "Prodromus literally means the northeast wind which blows for eight days before the rising of the dogstar," wrote Willis Linn Jepson. "The work was intended as a forerunner of that natural system which would sometime appear in effulgent glory. . . . The Prodromus blew for fifty years but the dogstar has not yet risen."[38]

Geopolitics dictates exploration. Banks and Solander were not welcomed when they visited Rio de Janeiro in 1769, and later Humboldt was forbidden to enter Brazil, then in tight control of Portugal. But Napoleon's invasion of Spain in 1807 set off independence movements in America. The tables turned in Portugal. Many left Lisbon for an emergent Brazil. The capital was moved from Bahia to Rio de Janeiro in 1808; Brazil was opened to English commerce, and the botanic garden was founded in that same year. For the succeeding decades a veritable parade of field-collecting explorers from Europe went to Brazil. Included were Langsdorff, Sellow, Saint-Hilaire, Pohl, Claussen, d'Urville, Mawe, Bowie, Burchell, Cunningham, and many more, a parade unmatched perhaps in the annals of botanical exploration.[39] The sixth German naturalist in the decade was Karl Friedrich Philip von Martius, born in Erlangen, northern Bavaria. Martius was joined by the zoologist Johann Baptist von Spix.[40] They traveled 1,400 miles from 1817 until 1820, on an expedition "that certainly ranks among the most important enterprises undertaken for scientific purposes in the [nineteenth] century." As many as 6,500 plant specimens, as well as living plants and seeds were sent to Munich. Zoological collections included 85 mammals, 350 birds, 116 fishes, and 2,700 insects. Seeded by the plant collections was the epic *Flora Brasiliensis*. Martius, then of age 46, prompted by the ill-fated Endlicher, in 1840 launched the first of 130 fascicles, which in 20,733 pages made 15 volumes. Martius completed 46 fascicles by his death in 1868. A. W. Eichler and Ignatz Urban continued to edit the *Flora* to its completion in 1906. Sixty five botanists of nine European nations contributed their accounts to *Flora Brasiliensis*.[41]

It may surprise us to read Asa Gray's letter to George Engelmann in 1863 that "Martius is not a very remarkable botanist, but good." Gray then added Martius "is a genial, philosophical soul (full of Plato, etc.), a good explorer, has worked up the Palms, etc., and is a wonderful man for the amount he knows on a vast number of different subjects—philology, antiquities, philosophy, *et id genus omne*."[42] Gray had first met Martius on his European tour in 1839—Gray was 28, Martius, 45, "a small man, not so tall as I" says Gray, "quite thin, but very good looking."[43] They met at the Royal Cabinet in Munich, once a Jesuit College, then containing the immense library, which according to Gray was one of the two largest in the world, though the collections except for the Brazilian plants "make no great show after that of Vienna." After his visit to the botanic garden, Gray dined at the "house of Martius," met his "very intelligent and pleasant" wife, and their four children. The party then retired to the royal chapel, listened to the chapel musician on the piano "play to perfection," then, says Gray, to crown all, Martius seized his fiddle, quite to my surprise, and played with great spirit."[44]

For the Brazil of Spix and Martius that will never return, listen to their "first night in the open air" not far from Rio:

> At Retiro, a miserable fazenda, lying sideways from S. Marcos, in a narrow swampy valley, surrounded by woody mountains, we passed the first night in the open air. The uraponga had ceased his strangely sounding notes, the swarms of grasshoppers commenced, as night set in, their monotonous chirp, at intervals interrupted by the notes of a large frog, resembling a drum, the lament of the capueira, and the dull cry of the goatsucker. Affected by the constantly returning impressions, we felt ourselves in a strange and solemn mood in the lonely wilderness, which was further increased when the filament, with all the splendour of the southern constellations, beamed on the dark forest, and millions of shining beetles fluttered in luminous circles through the

hedges, till at length a heavy rain veiled all in darkness.

The next mountains over which we passed are lower, and rise at intervals. The road is sometimes cut very deep in the soil, which consists of red clay, is very narrow, and when two troops of mules meet, as it often happens, dangerous. This kind of road is, however, welcome in luxurious forests, because confining all travellers to one narrow path, prevents it from being quickly overgrown, as would otherwise happen.[45]

No single botanist in this country accomplished so much in the Nineteenth Century to create the image of American botany as did Asa Gray. John Torrey, botanist, chemist, and mineralogist, differed from Gray, though they had characteristics in common. Both had a deeply religious turn of mind, although I have always suspected that Asa Gray attended Church as a proper Bostonian, whereas Torrey, a more retiring Christian, seldom mentioned his religious associations. Both took medical degrees, and both preferred the magnifying lens to the stethoscope.[46]

John Torrey wrote to Professor A. P. de Candolle at Geneva on January 6, 1837, "whenever I can find time I continue to work on my *Florae Americae Septentrionalis* on which I have been engaged for several years past. We are now doing much in N. America to perfect the Flora of our country." At this time he was expecting Gray to join the Wilkes Exploring Expedition. "Dr. Gray who has worked by my side for nearly three years past, is to be the botanist. He is well qualified for the situation. . . . The United States can well afford to send out this expedition as we have 50 millions of dollars in our treasury and have paid all our debts. I hope we shall yet have a national botanic garden. . . ."[47] Gray, however, declined, and together they proceeded with the *Flora*.

The *Flora of North America* was planned, fostered, and stands today as Torrey's monument, which Gray helped to raise. Gray worked hand in glove with Torrey, as Bentham and Hooker worked across the Atlantic. Gray's trip to Europe in 1838 was the first trip of an American botanist to visit European museums expressly to study type specimens essential to the writing of a flora.

By 1867 Asa Gray had many loyal followers with an almost idolatrous devotion. Frequent references in letters between botanists to "the Good Doctor Gray" attest to the fraternity of spirit. Gray had created a garden, a garden of living and dried plants, and by this time a garden of memories. It may fairly be said that he had even built an empire. To summarize Torrey's influence: he contributed to a sound taxonomy of the Cyperaceae; he fostered the work of many botanists including one, Rafinesque, with whom he disagreed; he wrote an exemplary pioneer state flora; and he prepared many descriptions of new species for the government-sponsored Mexican Boundary Survey and the Pacific Railway Reports. Torrey was 55 when they were begun.[48]

Asa Gray was a man of sound scholarship, broad culture, and of compelling personality, yet he was jealous of his preeminence. Alphonso Wood, with neither the talents nor the advantages of Gray, competed successfully in the textbook field.[49] The first edition of Wood's *Class Book of Botany* (1845) promptly sold out, the second edition and subsequent printings from stereotyped plates held their popularity. All the while the author was traveling and learning new floras. He made a major revision in 1861, and others followed throughout his lifetime. Altogether between 800,000 and one million copies of Wood's botanies were sold. Henry Nicholas Bolander, author of a catalogue of limited popularity on the plants of San Francisco area (1870), wrote enviously to Asa Gray in 1866, "What is to be done with Professor Wood?"[50]

Columbus Ohio bryologist Leo Lesquereux wrote to Professor Bolander in 1864 about an endemic feature of California: "We were greatly concerned about your shocks of earthquake and happy to know that you had escaped a living burial or something of that sorte."[51]

Who conquered the New World? For the naturalist there was no real conquest, only a quest. And the search continues. In 1841 George Bentham named the genus of plants *Heliamphora* based on Schomburgk's collection from Roraima. Today nine heliamphoras are known from the Guayana Shield.[52] The pigeonholes of this garden's herbarium hold verified undescribed taxa.

What of those "indehiscent capsules"? I taught plant taxonomy at Tulane, disseminating the definition that a capsule was dehiscent except when it was indehiscent, for example, in the Brazil nut. The American naturalist Herbert Huntington Smith wrote of the "nut-capsules . . . five inches in diameter and weighing two or three pounds; falling a hundred feet or more, they come crashing through the branches like cannon balls, and bury themselves often six inches deep in the ground. You can imagine," said Herbert Smith, "that a man's skull would be small proof against such a missile."[53] He had gone to Brazil at age 19 with his Cornell professor, C. F. Hartt, in 1870 and later collected off and on until 1902 in South America, Mexico, and the West Indies. In 1910 Smith became curator of the Alabama Museum of Natural History. Deafness

overtook him in time, and as he was walking on March 22, 1919 along a railroad track he failed to hear an approaching locomotive.[54] To get back to one of those indehiscent capsules, the poet Catullus in the first century BC wrote about what he called a "little chest"; he called it a *capsula* with no mention of indehiscence. John Lindley, master lexicographer, stressed the splitting in 1830, just as Leeuweuhoek in 1693 wrote of the "capsula breaking upon the ripening of the seed."[55]

Who really knows who conquered America? Can we encapsulate the story indehiscently? Definitions flow. *Omnia fleurit.* The pictures drawn of Barro do Rio Negro by Wallace and Spruce are different from the Manaus I saw in 1985. How long will the New World remain "new"? Capsules generally crack open, but what about the lecyths? They rot. Time is short and the water rises. Unfortunately one lifetime seems hardly enough to allow a scholar full mastery of every aspect of huge subjects like these. Peter Gayl, Dutch historian said: "History is an endless debate and he who delights in debates with historians enjoys the spice of historical writing." But, as Samuel Johnson said, "I may freely, without shame, leave some obscurities to happier industry, or future information."

Notes

2. Samuel Eliot Morison, *Admiral of the Ocean Sea: a Life of Christopher Columbus* (Boston, Little Brown, 1942) 2 volumes. 1: 60. One volume edition (1942) lacks the chapter notes.
3. *Ibid.* 1: 325.
4. Quoted in Carl O. Sauer, *Early Spanish Main* (Berkeley, Univ. California, 1966), 133. Morison, 2: 70, see map with dates following p. 68. J. Ewan, "The Columbian discoveries and the growth of botanical ideas with special reference to the Sixteenth Century" in *First Images of America. The Impact of the New World on the Old*, Fredi Chiappelli, editor (Berkeley, Univ. California, 1976), 807–812. References on pineapple, 812, note 14. Recent accounts: Francisco Oliva-Esteva and Julian A. Steyermark, *Bromeliaceaes of Venezuela, Native and Cultivated* (Caracas, Armitano, 1987), 100–101; Freddy Leal, "On the history, origin and taxonomy of the pineapple," *Interciencia* 14 (1989), 235–241.
5. Alfred W. Crosby, Jr., *Columbian Exchange. Biological and Cultural Consequences of 1492* (Westport, Connecticut, Greenwood, 1972), 171, 192.
6. *Ibid.*, 1985.
7. Morison, 2: 102–116.
8. Sterling A. Stoudemire, editor, *Oviedo's Natural History of the West Indies*, 1526 (Chapel Hill, Univ. North Carolina Studies Romance Languages and Literatures, 1959), 33. Amerindians used three body paints: red, from *bija* or *urucú* or *achiote* with variant spellings, the fruit of *Bixa*; bluish black, from *jagua*, or *genip*, *genipapi*, or *jenipapeiro*, *Genipa americana* L.; yellow, from bark of *Bixa*. See *Handbook of South American Indians*, Julian H. Steward, editor, (Bur. Amer. Ethnol. Bull. 143, 1948). 7 volumes.
9. Diagnostic phrase-names of Bauhin: *Arbor Mexiocana fructu castaneae coccifera. Pinax* (1671), 419.
10. Leonard Plukenet, *Almagestum botanicum* (London, 1696), 272. pl. 209, fig. 4.
11. A(lexander) S(mith) *in* John Lindley and Thomas Moore, *Treasury of Botany*, revised edition (London, Longmans, Green, 1889), 148.
12. Clements R. Markham, *Expeditions into the Valley of the Amazons, 1539, 1540, 1639* (London, Hakluyt Soc., 1859), 6–7.

12a. For Joseph de Jussieu in Ecuador see Arthur B. Steele, *Flowers for the King* (Durham, North Carolina, Duke Univ., 1964), 20–22; Frans Stafleu, *Linnaeus and the Linnaeans* (Utrecht Intern. Assoc. Plant Taxonomists, 1971), 278–279. For Jussieu's association with Lamarck see Ludwig Diels, "Beiträge zur Kenntnis der Vegetation und Flora von Ecuador," *Bibliotheca Botanica* 116, (Stuttgart, 1937), 48.

13. J. Ewan, "Early History" in J. Ewan, editor, *Short History of Botany in the United States* (New York, Hafner, 1969), 28. Nuttall commemorated Gambel in 1848 as *Gambelia speciosa* from his Santa Catalina collection made in February, 1847, but now = *Galvezia speciosa* (Nutt.) A. Gray. Witmer Stone, "Philadelphia to the coast in early days, and the development of western ornithology prior to 1850" *Condor* 18 (1916): 3–14. pp. 11–12. T. S. Palmer, "Notes on persons whose names appear in the nomenclature of California birds" *Condor* 30 (1928): 261–307, p. 278. Howard Campbell, "William Gambel, Naturalist" *New Mexico Wildlife* 26(6) (Nov.–Dec. 1978): 2–9, mentions Gambel's passing through St. Louis in April–May 1841, enroute to Independence, Missouri, but his diary (if any) is lost.
14. J. Ewan, "Notable living collections and botanic gardens" in Ian MacPhail, *Hortus Botanicus, the Botanic Garden and the Book* (Lisle, Illinois, Morton Arboretum, 1972), 118—119.
15. Emily W. Emmart, *Badianus Manuscript* (Baltimore, Johns Hopkins Univ., 1940). Martin de la Cruz, author of the Aztec text, latinized by Juannes Badianus. Pl. 20, p. 224, is *Datura meteloides* DC., not *D. arborea* L. Pl. 30, p. 234, *Philodendron* is perhaps *P. pseudoradianatum* Matuda but "not very close," not *Xanthosoma* fide Thomas Croat (pers. comm.).
16. John M. Fogg, Jr., "Two early cactus pictures," *Cactus and Succulent Jour.* 52 (1980): 267.
17. André Thevet, *Les Singularitez de la France antarctique* (Paris, 1558), Paul Gaffarel, annotated edition, 1878. P. Fournier, "au Bresil. André Thevet, cordelier," *Les Voyageurs naturalistes du clerge français avant la Revolution* (Paris, Lechevalier, 1932), 11–21.
18. *Annals Missouri Bot. Garden* 57 (1970): 92.
19. The widely cultivated, New World, narrow-leaved, showy-flowered *Thevetia peruviana* (Pers.) K. Schum. was one of three components of *Cerbera* in Linnaeus, *Sp. Pl.* (1753), 208–209. The second New World ovate-leaved "yoyote" or "yoyotl" is now *T. ahouai* (L.) A. DC. Linnaeus adopted the Indian name given

in Thevet's *Singularitez de la antarctique la France* (1588), 66. The third, Old World *Cerbera manghas* L., is now understood to comprise three elements, according to Herbert Huber *in* M. D. Dassanayake and F. R. Fosberg, *Flora of Ceylon* (Washington and New Delhi, 1983) 4: 53, 54. Such involved histories of Linnaean species are not unusual.

20. John Gerard, *Herball* (London, 1633, Johnson "emaculata" ed.), pp. 1545–1546.
21. Crosby, 177. See note 4. See also J. J. Finan, "Maize in the great herbals," *Annals Missouri Bot. Garden* 35 (1948) 149–191.
22. Joseph Ewan, "The Columbian discoveries and the growth of botanical ideas with special reference to the sixteenth century" in *First Images of America*, edited by Fredi Chiappelli (Berkeley, California, Univ. California Press, 1976), 2: 807–812, n. 4.
23. David Beers Quinn, "New geographical horizons: Literature" *in* Chiappelli, 635–658, Pp. 637–638.
24. Stoudemire, 86–87. See note 7.
25. J. & N. Ewan, *John Banister and his Natural History of Virginia, 1678–1692* (Urbana, Illinois, 1970).
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27. J. Ewan, "Plant collectors in America: backgrounds for Linnaeus" in *Essays in Biohistory* (Utrecht, Regnum Veg. 71. 1970) 22, 50. Fournier, 53–59 (see note 16). Typification problems reviewed by W. T. Gillis and W. T. Stearn, *Taxon* 23 (1974): 188–190. I. Urban, *Symbolae antillanae* (Berlin, 1898) 3: 62.
28. See note 26.
29. J. C. Beaglehole, *Exploration of the Pacific* (London, A. & C. Black, 1934, 3rd edition. 1966) and *Life of Captain James Cook* (Stanford Univ. Press, 1974), *passim.*
30. J. Ewan, "Silk culture in the colonies, with particular reference to the Ebenezer colony and the first local flora of Georgia" *Agric. Hist.* 43 (1969): 129–141.
31. Kristian Hvidt, *Von Reck's Voyage. Drawings and Journal of Philip Georg Friederich von Reck* (Savannah, Ga., Beehive Press, 1980), esp. 7–25. P. A. Strobel, *Salzburgers and other Descendents* (Baltimore, 1855, reprint, Athens, Georgia, 1953), 90–124. Pastor Henry Melchior Muhlenberg, mentioned as a visitor, not to be confused with botanist Rev. Henry Ernest Muhlenberg, who did not visit Georgia.
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34. Ewan (1969), 44–47. See note 29.
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52. Julian Steyermark, *Annals Missouri Bot. Garden* 71 (1984): 302.
53. Herbert H. Smith, *Brazil. The Amazon and the Coast* (New York, Scribners, 1879), 311. Jean de Laet described the tree, called *totocke* in *Novus Orbis* (1640), 632. Humboldt praised de Laet's "remarkable description," see Ewan (1976), 812 and note 3. *Bertholletia* fruits are "functionally indehiscent" fall to the ground, the seeds held inside by the smallness of the opercular opening or "plug" until the agoutis gnaw open the fruits, eat a few seeds, i.e. the "Brazil nuts," disperse others which may eventually germinate. See Scott A. Mori & G. T. Prance, Chapter 6 *in* R. E. Dickinson, editor, *Geophysiology of Amazonia* (New York, Wiley, 1987), 69–89.
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BOTANICAL EXPLORATIONS IN THE AMERICAN WEST—1889–1989: AN ESSAY ON THE LAST CENTURY OF A FLORISTIC FRONTIER

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Abstract

For many Americans the term "frontier" evokes images of cowboys and Indians, but for historians the "frontier hypothesis" is an explanation of the movement and evolution of people and institutions over time from settled urban areas into unexplored regions of remote wilderness. The hypothesis is predictive and may be applied to botanical explorations, the development of floristics models, and the evolution of systematic institutions. The earliest naturalists were lone generalists; they were followed by institutionally sponsored collectors in organized expeditionary groups. These naturalists typically presented their discoveries to urban-situated "professionals," who published the results. With the settlement of the frontier came local naturalists who published their own discoveries. Published floras evolved over time as each region became settled, with more details being included as the native plants became better known. Initially the first floras were expansive and general. These were followed by concise, descriptive local manuals, which evolved into multivolumed illustrated regional floras with a monographic format. The frontier hypothesis predicts that there should be a westward movement of institutional power caused by increased conservatism in the established eastern institutions coupled with a movement of talented people closer to the frontier. The hypothesis also states that when the frontier ends, there should be a rapid maturation of all institutions along with a reduction in their numbers, more specialization in their missions, a concentration of wealth and power to a few, and a greater uniformity of ideas expressed by all. The key to the future of systematic botany is to fight the tendency to suppress new ideas. With the end of the botanical frontier in the continental United States, the systematic community must decide how it will consolidate its institutions, what its missions will be, and how it will attempt to remain creative.

For many Americans the term "frontier" evokes the Wild West images of cowboys and Indians. Generations of pulp magazine readers, radio listeners, moviegoers, and now television viewers have grown up with the exploits of Buffalo Bill and Billy the Kid. To the younger generation who missed the weekly adventures of Roy Rogers and Trigger, the association of frontier with the American West might be an odd notion, so for them the concept might best be explained in terms of Hans Solo and the *Millennium Falcon*. No matter the cast of characters or the setting, it is the idea of a frontier that is important here—the concept of one or more adventuresome individuals searching for some unknown in a region that is itself largely unexplored.

The long-romanticized American frontier is distinct in character from the staid colonies of the eastern seaboard, and vastly different from that of Europe, where "frontier" alludes to a boundary between populous nations. The American character was shaped by the frontier experience and this in turn molded a unique civilization. No single event or feature can be credited with this; our European heritage of customs and institutions contributed but were changed by a mingling of peoples. All eventually were transformed by the industrial revolution and the economic and military growth of the United States into a world power. Taking a step back from these larger trends one finds, as the American historian Frederick Jackson Turner found nearly a century ago, that along the American frontier people and institutions underwent repeated rebirths of civilization at the raw edge of settlement during the four centuries required to cross the continent.

Turner formulated the "frontier hypothesis." He believed that one of the factors that drove the frontier westward from the fall line along the East Coast was the availability of free land on the edge of advancing settlement. Into that unoccupied wilderness came new immigrants who hoped to better themselves. With them came institutions and traditions of politics, economics, and religious and social customs. These were adapted to fit the more primitive conditions of the frontier, and as the

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frontier moved even further west these modified institutions and traditions changed again.

The primitiveness of the frontier's edge did much to force the reshaping. Highly developed institutions and customs gave way to more simple associations and more pastoral pursuits. After the third century of westward expansion, reaching, as the great arch in St. Louis now symbolizes, the beginning of the trans-Mississippi West, the people, institutions, and customs were already significantly different. Each generation on the advancing frontier had transformed its antecedent with an evolutionary selective process as significant as any seen in the biological world. Adaptation and change were common to all aspects of the frontier existence.

Laws and customs were based on those found just to the east on what previously had been a line of frontier settlement. As each frontier community became more settled, the structure of the institutions became more complex and local customs more sophisticated. Governments and institutions became rigid and conservative with the economic structure specialized. Religious and social customs became stratified into specific beliefs and social classes. In turn, these would be contributed to the adjacent community forming on the edge of the wilderness in a freer, less-sophisticated, and more rebellious form.

Coupled with this was the imposition of the ever-changing local climate and environment. Just as there were continuous rebirths of civilization on the edges of the American frontier, so too did new ways and customs evolve and adapt to the changing environment. To Turner this was significant for it resulted in the "Americanization" of people, customs, and institutions. The American character, he felt, was the result of the evolution and adaptation of society to fit the ever-changing physical environment.

Into this grand equation we now place the plant explorer. By examining this minor character we might better understand: the field of American systematic botany; the historical significance of the large eastern institutions and why it is that the power base is moving westward; the causes leading to an increase in conservative thought and the narrowing of the power base to a few; the increasing failure of institutions with an historical mission of supporting systematics; the concentration of funding and opportunities to do research; and the fleeting importance of the methodologies promoted by the different factions in systematics. Perhaps then we might also better contemplate the future, for as Turner dated the end of the American historical frontier as 1890, so too must we now date the end of the American floristic frontier as 1990.

What lies beyond is our future. Much as Butch Cassidy and the Sundance Kid left Utah to find a more exciting frontier, so too are many of our systematists leaving temperate North America for the wilds of South America. This is not unexpected because the frontier hypothesis predicts it should be so. In the continental United States we have a known flora and an ever-dwindling number of novelties. With the disappearance of our floristic frontier, so too are those who long for the excitement of the unknown and the thrill of discovering new frontiers.

Botanical Explorations and the Frontier Hypothesis

To a significant degree, botanical exploration in the American West is as much a tale of romance and adventure as that of any fur trapper or cowboy. The tales of those who risked life and limb to find a plant simply for its uniqueness and beauty have long been the stuff of novels and television movies.

The first botanical explorers in temperate North America were lone individuals who were nearly always transients. Many were ship's surgeons or ministers. Others were members of the military, surveyors, physicians, or wives. Some collected to win a favor from one of Europe's rich and powerful. But there were real collectors, too, who sailed to America and probed the rich forests along the great rivers and onto the backbone of the Appalachian Mountains. No sooner had paths been pushed through these mountains than naturalists were along them, collecting whatever they could find.

Both the Atlantic and Pacific coasts had early explorers. In the 1600s, plants from the colonies were taken to Europe. A century later, ships from several nations roamed the inlets of the West Coast gathering all kinds of plants, not just trees and shrubs as had been the trend prior to the 1720s. For most Europeans, interest in the flora of eastern North America waned after 1700 with the discovery of the horticultural treasures found in China and Japan, and even the West Coast of North America attracted little interest until the diversity of the inland forests became known in the 1820s. Still, naturalists came.

For the new nation of the United States, science was largely neglected until the presidency of Thomas Jefferson. Jefferson sought and obtained congressional support for a party of explorers to venture up the Missouri River and to cross the

mountains to the Pacific Ocean. They were to survey the natural history and to observe the native peoples and their customs. The land was to be mapped, the features named, and the geology understood. Thus, Lewis and Clark explored the wilderness beyond the frontier at the mouth of the Missouri River. The plants they found were destined to be taken to Europe, described by foreigners, and essentially lost for nearly a century.

Other expeditions followed. One went up the Red River of the Arkansas and another followed the Arkansas itself. Neither was successful scientifically. William Bradbury and Thomas Nuttall, each associated with competing trading companies, traveled up the Missouri River in 1811 to the Mandan villages of North Dakota, but the War of 1812, more thievery, and other unforeseen fates befell the men and their collections, rendering them less significant than they might have been.

On the West Coast, after half a century of coastal explorations by the French, English, and Russians, David Douglas explored the interior and collected hundreds of new species, many of which made their way into European gardens. Like the fur trapper's beaver pelts that were taken to foreign lands where others profited, so too were North American plants sent to Europe where they were described and classified. The exploitation of our natural resources is predicted by the frontier hypothesis and is expected at this stage of development on any new frontier.

European naturalists who sought plants in the North American wilderness after 1800 were often supported by scientific organizations, companies, groups of wealthy men, or governments. For the new nation, there were few formal organizations able to support natural history expeditions, and with almost no wealthy class the task fell mainly to the federal government. Only after the cream of the botanical novelties had been gathered by others did American scientific expeditions begin to move across the continent. Previous generations had found the obvious; this one collected critically.

The year 1850 was significant for by then the frontier was west of the Mississippi River. The gold rush to California was at its height. Texas had been added to the nation, the Oregon question settled, and the land from the crest of the Rocky Mountains to the California coast acquired as a result of a war with Mexico. No sooner had the frontier come within sight of the western boundary of the United States than a vast new wilderness was added to the nation's map. Still, there were scattered settlements on the fringes. The Oregon, California, Mormon, Santa Fe, and Spanish trails were in constant use. Farming communities had been established in the Central Valley of California and the Willamette Valley of Oregon, and the Mormons had arrived in Utah. The small mission villages along the California coast from San Diego to San Francisco had been augmented by a series of boom towns dotting the foothills of the Sierra Nevada, and gold and silver would soon be found elsewhere. To the north, the old forts of the Hudson Bay Company were giving way to new fishing, lumbering, and farming communities.

As before, naturalists came to the frontier, crossed it into the botanical wilderness, but in doing so came to a new frontier moving eastward. The unexplored regions of the American Southwest and the Great Basin attracted greater attention, with the two massive cordillera, the Rocky Mountains, and the Sierra Nevada-Cascade Range bringing many to search for their novelties. Government expeditions to map the interior of the American West provided numerous opportunities for naturalists to explore remote regions. On both edges of the frontier, institutions were being established, indicating a higher generational order near the frontier. In St. Louis, George Engelmann and Henry Shaw were joining forces and the forerunners of the Missouri Botanical Garden were taking shape, while in San Francisco, a group of naturalists led by Albert Kellogg were coming together to establish the California Academy of Sciences.

The Civil War years of the 1860s, and then a decade of Indian wars in the 1870s, took their toll on scientific efforts. Many naturalists who might otherwise have gone west in search of scientific curiosities were delayed or hesitant. When the turmoil ended, many went west, some to become local amateur naturalists, some to be professional collectors, and a few to serve in the new scientific military or to join the few academic institutions offering botany. In time, as Congress reduced the role of the military, more and more of the scientific research done in the wilderness was carried out by civilian agencies.

By the 1870s, the wilderness beyond the frontier was restricted to the Rocky Mountains, Great Basin, and desert regions of the Southwest. Into these areas, as predicted by the frontier hypothesis, came lone naturalists in this rebirth of civilization on the botanical frontier. This generation was more educated and critical than previous ones, reflecting the increased sophistication of their immediate ancestors. Some were supported by the federal government, but many were associated with colleges or

with scientific institutions. To a lesser extent, some were private collectors interested in selling their specimens. Most came to the frontier and entered the wilderness only for the growing season, but by the 1880s, some devoted all of their energy to settling the American, as well as the botanical, frontiers.

In its simplest form, the closure of the American frontier in 1890 was signified by the settlement of the land by people. The botanical frontier lagged behind for there were still remote regions to be explored for their botanical treasures. The lure of new species drove naturalists into the wilderness where the discovery of novelties was still routine. For the botanical frontier to close, those remote regions had to be explored and their botanical novelties discovered.

The Closing of the Botanical Frontier

The last century of botanical explorations and discoveries, the writing of floras and florulas, and the development of today's botanical institutions did not occur in a vacuum. There was a past, and that past molded what is in the present. Numerous collectors came to temperate North America before and during the Linnaean era, and these collections were used by Carl Linnaeus to describe nearly 900 species from temperate North America in his 1753 two-volume work, *Species Plantarum*; the majority were based on specimens obtained by just two men, John Clayton and Pehr Kalm. Even the majority of North American plants named by Linnaeus after 1753 were based on the collections of John Bartram alone.

The exploits of post-Linnaean naturalists in eastern temperate North America did much to settle that floristic frontier by 1825 with Thomas Walter, John Fraser, André Michaux, Frederick Pursh, Thomas Nuttall, Stephen Elliott, Jacob Bigelow, John Torrey, and Amos Easton being major contributors to the effort.

While Nuttall continued to explore on the edge of the frontier, Torrey remained in the floristically settled East where he rose to a position of influence and became the first to dominate systematics in temperate North America. That mantle was soon passed on to Asa Gray at Harvard University, who became the single most influential man in our frontier history. Together, Torrey and Gray imposed their will up to 1889.

To settle in a wilderness is not to conquer it. Although Torrey and Gray did much to describe the flora of temperate North America, much like Linnaeus before them, they too relied upon others to discover the novelties. It was those people who closed many of the botanical frontiers across the continent.

For the Northeast, Torrey and especially Gray made substantial contributions. They were followed at Harvard by Sereno Watson, Benjamin L. Robinson, and Merritt L. Fernald, all of our "century," 1889–1989. These men had a competitor in the form of Nathaniel Lord Britton and later Henry A. Gleason at the New York Botanical Garden. Each man championed a series of flora projects, students, and institutions as shall be noted below. The honor of closing the floristic frontier in the Northeast, however, must be granted to Fernald. In 1950, following nearly half a century of devoted fieldwork on his part and a careful study of type material, Fernald published a fitting tribute to all who had followed Asa Gray.

The richness of the southeastern United States was discovered initially by the likes of Mark Catesby, Thomas Walter, and the father and son teams of Bartrams and Michauxs. Overlapping our century were Alvan W. Chapman, Samuel B. Buckley, and John L. Riddell. John K. Small did much to reduce the botanical frontier in the South during the first half of our century, but only now, thanks to the efforts of Robert W. Long, Olga K. Lakela, Robert K. Godfrey, Daniel B. Ward, and Walter S. Judd in Florida, Albert E. Radford, C. Ritchie Bell, and their colleagues in the Carolinas, and Delzie Demaree, Robert Kral, M. Murray Evans, and R. Dale Thomas elsewhere in the South, has its botanical frontier closed.

The flora of the Old Northwest was almost always considered synonymous with that of the Northeast, a fact reflected by the regional floras of the area. The university community was active in the search for new species, but the individuals were largely dominated by those at Harvard and New York. State floras were written and are now being written, but without a definable region where novelties are to be expected, one must conclude that the botanical frontier ended in 1950, when it closed in the Northeast.

Early plant explorers on the Great Plains were mainly transients who hurriedly crossed the region to get to the mountains of the West. The Great Plains were the deeded home of many American Indians, and travel off established routes was rarely done. With the gradual demise of the Plains Indians, and in the 1860s and 1870s the loss of their homeland, plant explorers were able to penetrate beyond the limits of the frontier trails established by the cattlemen, miners, and cavalry. Even the

resident naturalists were often transient. Albert S. Hitchcock left Kansas for Washington in 1901, and Per Axel Rydberg left Nebraska in 1895, eventually accepting a position at the New York Botanical Garden in 1899.

Unlike in the Old Northwest, specimens collected by resident plant explorers on the Great Plains tended to remain in local university herbaria. This was, in part, because the Great Plains were sufficiently far enough removed from the eastern centers to evoke a degree of independence, but also the men and institutions themselves had come from a more isolated, former frontier. Persons like Charles E. Bessey in Nebraska and Theodore D. Cockerell in Colorado collected for years, trained numerous students, and built large herbaria. To be sure, outsiders continued to come to the Great Plains, and there were other resident naturalists who collected throughout much of the area, yet credit for closing that botanical frontier must be granted to the late Homer A. "Steve" Stephens, who made some 90,000 collections before he retired in 1975.

Botanical explorations in Texas began in 1828 with Jean Louis Berlandier, who was followed by Thomas Drummond in 1833, by Ferdinand J. Lindheimer, Auguste Trécul, and Charles Wright in the 1840s, and by Julien Reverchon, who collected from 1870 to 1885. The remarkable diversity across the state, to say nothing of its size, meant that the botanical wilderness in Texas was more a series of pockets than a single definable line. The work of Victor L. Cory, Lloyd H. Shinners, Barton H. Warnock, Frank W. Gould, Donovan S. Correll, Billie L. Turner, and Marshall C. Johnston led ultimately to a 1970 flora of Texas and brought its floristic frontier to an end.

The West Coast floristic frontier differed dramatically from its eastern counterpart in many aspects besides the great diversity in its flora. Here naturalists were often far in advance of others in the exploration of the West, and the naturalists demonstrated their independence and adventuresomeness by their very presence. Most significant of all, they were well isolated from the eastern establishment so that they were able to make critical decisions on the future of their profession.

At first the discoveries were slow. Jean-Nicolas Collignon collected the first plants near Monterey, California, in 1786—some 280 years after the first plants were taken to Europe from the East—and Jean Baptiste Lamarck described the first trans-Mississippi species, *Abronia umbellata*, in 1791. The Spanish, English, Russian, and American governments sent other botanical explorers to the West Coast so that the roster of collectors grew rapidly, but it was David Douglas who was destined to be the most formidable, for he forced the botanical frontier away from the Pacific Ocean. Others entered the Pacific Northwest by land, following the Oregon Trail with Nathaniel J. Wyeth, Thomas Nuttall, Karl A. Geyer, and John C. Frémont following that same route. Since 1889, many have devoted much of their professional life to closing its botanical frontier.

In Washington, Wilhelm M. Suksdorf, Charles Vancouver Piper, R. Kent Beattie, F. Marion Ownbey, and Harold St. John explored many parts of the state. Fieldwork was done in Oregon by Thomas Jefferson Howell, William C. Cusick, and Morton E. Peck, with lesser contributions made by Louis F. Henderson and LeRoy E. Detling. More recently, Helen M. Gilkey and Kenton L. Chambers and their students and associates have been actively collecting in the state. In adjacent Idaho, naturalists tended to pass through the region rather than explore it for its novelties. Still, the team of John H. Sandberg, John B. Leiberg, Daniel T. MacDougal, George Vasey, and Amos A. Heller collected extensively in northern Idaho around the turn of the century. Louis F. Henderson of the University of Idaho concentrated his efforts in eastern Idaho, and Aven Nelson of the University of Wyoming and several of his students, including James F. Macbride and Edwin B. Payson, collected in Idaho during the first two decades of this century. John H. Christ of the Soil Conservation Service collected nearly 10,000 numbers in the 1930s when Ray J. Davis, who started the herbarium at Idaho State University in 1930, was encouraging others to collect. Among Davis's students were Arthur Cronquist and my own father, Jack L. Reveal, who gained a lifelong appreciation of grasses from Davis.

The team of C. Leo Hitchcock and Clarence V. Muhlick actively collected throughout the Pacific Northwest. It is to them and to 1973, when Hitchcock retired, that one must credit the closing of the floristic frontier in the Pacific Northwest.

The diverse flora of California has long attracted botanists. Its botanical frontiers moved away from the coast into the mountains and deserts early in its history so that California had its own published flora by the mid 1870s. The cast of post-1889 characters was, and even today is, remarkable.

Mary Katherine (Curran) Brandegee and Alice Eastwood are two of the more notable characters. Both collected actively throughout much of the American West. Their lives were closely interwoven as Eastwood succeeded Brandegee, in 1894,

as the curator of botany at the California Academy of Sciences. Both had ardent followers and supporters, and each in turn promoted botany as a science. The university scene was equally gifted with the likes of Willis L. Jepson, who replaced Edward L. Greene in 1895, and like Eastwood, remained active in botanical explorations for half a century. At Stanford University, the reign of William R. Dudley began in 1892, with LeRoy Abrams joining the staff in 1902. Berkeley and Stanford graduated many students who continued explorations in California. Jepson students included Harvey Monroe Hall, who graduated in 1906; Ivan M. Johnston, John Thomas Howell, David D. Keck, and Conrad V. Morton, all of whom graduated in the 1920s; and Lincoln Constance, who finished his degree in 1934. Herbert L. Mason went from Stanford to Berkeley, receiving his doctoral degree in the early 1930s whereupon he joined the Berkeley staff. Also from Stanford were such active collectors as Elmer I. Applegate, Ira L. Wiggins, Charles Piper Smith, and Roxana J. Ferris.

Numerous collectors were associated, in some fashion, with each of the three institutions in the San Francisco Bay region. At the Academy, where John Thomas Howell held the curator's chair after Eastwood, numerous knowledgeable "amateurs" came for guidance. The list is long, but one cannot ignore the likes of Ernest C. Twisselmann, Gordon True, or Gladys L. Smith. Samuel B. Parish and Charles Russell Orcutt, both active in southern California from the 1880s until the 1920s, contributed their personal herbaria to Stanford. Adolph D. Elmer collected widely in California, with his specimens going to Stanford.

Numerous individuals were attracted to Berkeley. Ethel K. Crum, Annetta M. Carter, Helen K. Sharsmith, and Lauramay Dempster each made significant collections. Contributing their herbaria to Berkeley were such collectors as John Gill Lemmon, Joseph P. Tracy, and Ira W. Clokey. In addition to the large collections made by Jepson, Mason, Constance, and more recently Robert Ornduff, who were on the Berkeley faculty, the efforts of Jepson Herbarium staff, notably Rimo Bacigalupi and Lawrence R. Heckard, made great inroads into many rarely collected portions of California.

In southern California, Pomona College came to be the focal point of plant explorations and systematics. Philip A. Munz, who became director of the nearby Rancho Santa Ana Botanic Garden, was deeply involved in floristics. From 1917, when he joined the college's faculty, until his death in 1974, Munz was devoted to the California flora and made numerous collections. His students read like a "who's who" in plant explorations both in California and beyond: F. Raymond Fosberg, C. Leo Hitchcock, George J. Goodman, David Keck, and Louis C. Wheeler are just a few. Munz concentrated his efforts in the mountains and deserts of southern California, but made occasional excursions to the North. His student and eventual colleague Lyman D. Benson was also a formidable collector, albeit more specialized.

The basis of the Pomona College Herbarium was the private herbarium of Charles F. Baker, who amassed a collection of some 100,000 specimens. To this, Munz added the herbarium of Marcus E. Jones in 1923; it too numbered approximately 100,000 sheets. The collections of Frank W. Peirson, M. French Gilman, Percy C. Everett, and Carl B. Wolf may now be examined at the Rancho Santa Ana Botanic Garden.

In the years since Munz died in 1974, many new species have been found by persons willing to explore the most remote portions of California. Mary C. DeDecker discovered *Dedeckera*, which was described in 1976, and James R. Shevock is still uncovering novelties. Yet, the finds are few and generally scattered so that it seems appropriate to close California's botanical frontier in 1976, a century after the state's first flora was published.

The Rocky Mountains have always attracted the botanically curious. When Joseph Dalton Hooker came to America in 1877, Asa Gray took him to the Rockies. Numerous naturalists came by train to spend the summers in the coolness of their height and to regale in their splendor. In 1889, no other region of the United States was attracting such a diversity of botanists. Per Axel Rydberg, Marcus Jones, and Joseph W. Blankinship did much to explore previously unstudied portions of Montana, with Charles Bessey sometimes joining Rydberg. C. Leo Hitchcock collected in western Montana, especially during his tenure at the University of Montana from 1932 until 1937. Several university-based professors and their students have climbed the mountains in search of plants, with the "amateur" Klaus Lackschweitz among the forefront of recent collectors.

Aven Nelson is synonymous with floristics and Wyoming. This remarkable man, a botanist, teacher, and president of the University of Wyoming, was productive throughout his 97 years. He collected widely in the state, expanding its floristic frontier away from the narrow Oregon Trail and Central Pacific Railroad route where nearly all before him had concentrated their efforts. He encouraged others to collect, and the students he influenced to continue in systematic botany are

now legendary: Elias E. Nelson, Leslie N. Goodding, James Francis Macbride, Edwin and Lois E. Payson, George J. Goodman, Louis O. Williams, and Reed C. Rollins. C. L. Porter, who came to the University of Wyoming in 1929, continued the tradition of exploring the wilds, concentrating in the 1930s on bryophytes and then vascular plants. The massive field efforts by Ronald Hartman in the 1980s, although still demonstrating the need for additional fieldwork, have conquered the last vestiges of a botanical frontier in Wyoming.

The Colorado Rockies have been a beacon to naturalists since the first specimens were taken by Thomas Say and Edwin James in 1820. The work of Cockerell, Rydberg, Charles Penland, George E. Osterhout, Harold D. Harrington, and a host of others who have explored the Rockies since 1889 have allowed William A. Weber of the University of Colorado, long a persistent and diligent collector, to be the last to collect on its botanical frontier.

Across the American Southwest, the floristic frontier moved slowly, being pinched in from both the East and the West. The first to collect in New Mexico was William Gambel, who traveled the Old Spanish Trail from Santa Fe to Los Angeles. During the war with Mexico, Major William H. Emory, Lieutenant James W. Abert, and Charles Wright entered New Mexico, collecting specimens whenever possible. Augustus Fendler and Friedrich A. Wislizenus arrived in Santa Fe with Emory and his "Army of the West"; Fendler remained in New Mexico collecting in the mountains to the north while Wislizenus turned southward into Mexico. Thomas Coulter was the first to explore Arizona botanically, visiting Yuma in 1832. Naturalists associated with other military expeditions, and especially the Corps of Topographical Engineers, discovered numerous botanical novelties. The most important collector of our "century" was Edward Palmer, who gathered plants in the Southwest for nearly 40 years. Others have searched for plants, with many finding a surprising number of novelties in the more remote regions since 1930. The floristic frontier in the Southwest was gradually reduced through the efforts of Forrest Shreve, Thomas H. Kearney, and Robert H. Peebles. The botanical wilderness finally disappeared along the border of central Arizona and New Mexico in the 1980s through the efforts of Donald Pinkava in Arizona, Richard Spellenberg in New Mexico, and their many colleagues and students.

The floristic frontier swept into the Intermountain West from all directions. The historical California and Spanish trails to the Pacific Coast had been rapidly botanized prior to 1889. Like in the Southwest, many military-sponsored expeditions crossed Utah and Nevada, with the geological surveys led by Clarence R. King, and especially by John Wesley Powell and George M. Wheeler, putting their botanists into exceedingly remote areas. The university communities in Utah and Nevada encouraged botanical explorations by their faculty, and the faculty in turn encouraged numerous students. Among the more significant were Amos A. Heller and Patrick B. Kennedy of the University of Nevada, and Walter P. Cottam and Seville Flowers of the University of Utah.

The post-1889 history of botanical explorations in the Intermountain West cannot be told without a brief mention of Marcus Eugene Jones. He set out to explore the whole of the "Great Plateau," as he termed the Intermountain West, and succeeded in traveling throughout most of it. He collected wherever he went and described many narrowly endemic species as he amassed his herbarium. While Jones lived in Salt Lake City (1880 to 1923), he carefully guarded the frontier with his biting pen and his quick printing press. Those who ventured upon his territory were all too often destined to be the subject of his scorn. His desire to write a "Flora of the Great Plateau" eluded him, however, and the manuscript was still unfinished when he died in a car accident in 1934.

Many botanical teams came to the cold deserts in search of plants. Eastwood and Howell were active in the 1930s and 1940s, with H. Dwight Ripley and Rupert C. Barneby, Bassett Maguire and Arthur H. Holmgren, and Annie Alexander and Louise Kellogg continuing the trend into the 1950s. Noel Holmgren and I collected together in the 1960s, with N. Duane Atwood and Larry C. Higgins replacing us in the 1970s. Arnold "Jerry" Tiehm and Margaret Williams, working mainly in Nevada, were active in the 1980s.

Stanley L. Welsh and his students and associates at Brigham Young University moved the floristic frontier westward across Utah into Nevada, closing it for Utah in 1987. In Nevada, Tiehm, who discovered a wealth of new species in isolated portions of Nevada, completed the task and may be considered the last to have explored on the botanical frontier in the continental United States.

The Evolution of Floristic Styles on the American Frontier—1889–1989

Many of the early floras treating the known plants of the world included species that had been collected on the edge of whatever frontier existed at the time. Among the early settlers were men

and women willing to collect natural objects for others to study. Occasionally, some desired to publish their own findings, but events and others usually conspired to prevent this, as happened to John Clayton whose manuscript of the flora of Virginia was published by Gronovius, with the help of Linnaeus, in 1739 and 1742. Forty years later, Thomas Walter's *Flora Caroliniana* was edited and published in London by John Fraser. The French naturalist, André Michaux, who explored on the edge of the frontier in eastern Canada and the United States, did write his own 1803 *Flora Boreali-Americana*, but many still believe it was actually the work of L. C. Richard. One of the first American books devoted to the plants of a region was the little-known 1808 *Flora Carolinaeensis* published in Charleston, South Carolina, by John Shecut. This work was designed for the physician. It contains excellent descriptions and surprisingly well-informed distribution statements. Only one of its two volumes was published. Frederick Pursh, after spending several years in the United States, published his 1814 *Flora Boreali-Septentrionalis* in London.

Most floristic manuals treating the plants of temperate North America prior to 1814 were at best general approximations of the diversity. The style was Linnaean—short descriptions and a brief statement regarding distribution—as was the classification (Shecut being an exception in all respects). Both were dictated by strong historical ties with England and the influence of James Edward Smith and others of the "Linnaeans" then in London. The transition in styles and formats may be seen in the 1814 *Florula Bostoniensis* by Jacob Bigelow, who maintained the concept of the Linnaean diagnosis, but added a more detailed description for those plants he knew from the field. He also provided a common name for each species. In *A Synopsis of the Genera of American Plants* published in Georgetown by J. M. Carter, also in 1814, one finds a key to the classes and orders, but the descriptions themselves are classically Linnaean.

In Stephen Elliott's *A Sketch of the Botany of South-Carolina and Georgia* (1816–1824) the diagnoses are expanded and given in both Latin and English. A full description of each species was given with the characters arranged in a manner not unlike a modern flora. Elliott provided information on abundance and the time of flowering, and cited previous places of publication and illustrations.

The use of "natural orders," or what we would term "families," in floras was highly debated at this time. Most works, such as William Barton's *Compendium Florae Philadelphicae* and Thomas Nuttall's *Genera of North American Plants*, both published in Philadelphia in 1818, followed the Linnaean system with the genera artificially arranged in nearly 60 classes and orders. In 1789, A. L. de Jussieu had proposed 100 natural orders, and these were coming into use, especially in Germany. The first North American work to use natural orders was *Florula Ludoviciana*, published in New York by Constantine Rafinesque in 1817. Two years earlier, Rafinesque had proposed more than 300 natural orders. Amos Eaton was more cautious in his 1817 *Manual of Botany*. He arranged his plants following Linnaean principles, but in his introduction he presented an outline of the Jussieu system, complete with descriptions, representative genera, and medical uses. He also provided a glossary. Unique to this work, the genera were described in one section with the species accounted for in another. A habitat statement was given, but where in "the northern and middle states of America" the plant was found was not provided.

Torrey's *A Flora of the Northern and Middle Section of the United States*, dedicated to Thomas Nuttall, appeared in 1823 and 1824. True to his heritage, he arranged plants in the Linnaean fashion. The genera were briefly described, with references given to previously published descriptions and synonymy. He also provided a common name. However, he noted the natural order that each should be assigned.

The professional union of John Torrey and Asa Gray was to alter immediately the style of American floras. The Americans were no less grandiose in their plans for continental floras than their European counterparts. The first part of William Jackson Hooker's *Flora Boreali-Americana* appeared in 1833, and in 1838 Torrey and Gray began their own never-finished *A Flora of North America*. Like other efforts of its kind, the project suffered from an overwhelming amount of new material that could not be readily summarized.

For the evolution of floristic models, however, this was to be a significant work. The usefulness of natural orders in classifying plants had been amply demonstrated by John Lindley in 1830, with the publication of his *Introduction to the Natural System of Botany*, and he had swept away the last influences of the Linnaean sexual system on plant classification. Gray was an ardent follower and incorporated the concept in the *Flora*, going so far as to provide dichotomous keys to the families based on those in Lindley's 1835 *A Key to Structural, Physiological, and Systematic Botany*, and even to genera as seen in S. F. Gray's *A Natural*

Arrangement of British Plants (1821). There were no keys to the species; rather, Torrey and Gray provided diagnostic headings to groups of species following the format designed by A. P. de Candolle for the *Prodromus*.

More practical regional floras began to dominate the floristic scene, with the majority written for the settled portions of the United States. John Darby published *A Manual of Botany Adapted to the Productions of the Southern States* in 1841. Gray responded in 1848 with the first edition of his *Manual*, which was a comparable treatment for the plants of the northern states. The first edition of Chapman's *Flora of the Southern United States* was published in 1860. In all of these works, the plants were arranged in families, keys to the families were provided, and some means were provided which allowed one to discriminate among the various groups of species. Works for students began to appear as well. Gray published the first edition of his *Elements of Botany* in 1836. Alphonso Wood's *Class-book of Botany*, initially published in 1845 and variously titled, underwent many revisions and editions, selling perhaps a million copies over the next 50 years. For those at female seminaries there was Mrs. Lincoln's *Familiar Lectures in Botany*. Gray and Wood followed Lindley. Wood's key to the families, however, was bracketed and only partially dichotomous; Mrs. Lincoln tended to retain the Linnaean model.

In addition to floristic studies, a growing number of naturalists began to specialize on groups of plants. Mosses, bryophytes, ferns, grasses, and even certain genera of flowering plants became the focus of intense study. As Gray's career evolved during his lifetime, he too became an authority on a multitude of families (notably Asteraceae) and such diverse genera as *Eriogonum* and *Penstemon*.

For those who were on the western frontier, however, the aging Gray eventually became an impediment as he seemed to become increasingly more rigid and demanding that his authority not be questioned. To the independent westerner this was intolerable, and a revolt began in the form of defiance by Edward L. Greene, Marcus E. Jones, and others who lived and worked on the floristic frontier. It was traditional for most new species to be sent to Gray for evaluation and approval. After the mid 1870s, evaluation was left to Sereno Watson who, like Gray, was at Harvard University. Approval was not guaranteed. Furthermore, editors often submitted articles to Gray or Watson for comment. Some westerners alleged that their new species were thus delayed awaiting Gray or Watson to describe the same plant from material in their own holdings. Later, Per Axel Rydberg required some western authors to submit vouchers with their manuscripts so that he could make his own evaluation of their new species. It was this pretense of eastern superiority that many on the floristic frontier resented and rebelled against. The result was sectionalism and its expression was in the form of a host of privately published journals.

Books, manuals, and regional floras were difficult to write and expensive to publish on the frontier. Most westerners had limited resources and thus it was simpler to publish new species. Botanical journals are, even today, the bread and butter of the systematic community, but they were not common prior to 1900 and most were restrictive in some fashion. The *Transactions of the American Philosophical Society*, one of the first American journals, began in 1771, and the *American Journal of Science* started in 1818. The *Proceedings of the American Academy of Arts and Sciences*, long the journal used by Gray and Watson, began in 1846. Institutional journals first appeared in 1817 when the *Journal of the Academy of Natural Sciences of Philadelphia* was established; it was followed by *Smithsonian Contributions to Knowledge* in 1848. Some local and regional western American academies had their own publications. The *Proceedings of the California Academy of Sciences* published its initial volume in 1854. The *Transactions of the Academy of Science of St. Louis* had its origin in 1860. Current journals, such as the *Bulletin of the Torrey Botanical Club*, began in 1870; this was soon joined by the *Botanical Gazette* in 1875 and *Rhodora* in 1899. These three eastern-dominated and establishment-sponsored journals were soon the primary outlets for individuals who were not associated with an institution to propose new species. With the advent of open journals, the institutional ones often became largely even more restricted. Examples include the Smithsonian's *Contributions from the United States National Herbarium* (1890), Harvard's *Contributions from the Gray Herbarium* (1891), Chicago's *Publications of the Field Columbian Museum* (1895), and the *Bulletin of the New York Botanical Garden* (1896). The ancestor to the *Annals of the Missouri Botanical Garden*, which began in 1914, was the *Annual Report of the Missouri Botanical Garden* (1890).

To isolated, independent westerners, these journals were either unavailable or the editorial policies made it difficult for them to publish their findings. To a substantial degree each journal was edited by a strong personality who had political, economic, or institutional reasons for excluding the works of

outsiders. Most of the dissidents had earned their reputation as a "botanical pest" (to quote one of them speaking of another) so that very often there were sound scientific reasons why an editor should be cautious. As a group, the westerners were a quarrelsome lot—if one made an error, another would immediately write the editor to complain.

Another factor for the independent western journals, and one predicted by the frontier hypothesis, was the need to establish an independent identity. What better way than by a scientific journal? The proliferation was immediate: Greene began *Pittonia* in 1887, Townshend S. Brandegee and Mary Katherine Brandegee started *Zoe* in 1890, and Jepson released the first issue of *Erythea* in 1893. Heller started *Muhlenbergia* in 1900, and Marcus Jones began his *Contributions to Western Botany* series in 1902.

With Gray's death in 1888, one year before our "century" began, the domination of the eastern establishment weakened and Watson, Robinson, and Fernald, who followed Gray at Harvard, never gained his stature and respect. Britton and Rydberg at New York, and John Merle Coulter in Washington, further weakened Harvard's importance by imposing their own forms of domination.

Still, western floras were written. The initial efforts came in the form of a cooperative effort between a university and a state agency. William H. Brewer of the California Geologic Survey and Watson of Harvard University published the first volume of their flora for the state in 1876. Volney Rattan followed with his privately published *A Popular California Flora* in 1879. Greene, who became professor of botany at the University of California in 1885, privately published the first part of his *Flora Franciscana* in 1891. At Wabash College, Coulter compiled a *Manual of Botany of the Rocky Mountain Region*, which was published in 1885. These floras followed the format developed by Gray for his *Manual*. There were no innovations except by Brewer and Watson, who had sections devoted to discussion much as seen in Torrey and Gray's *Flora*, but heretofore not found in a local flora.

Prior to 1900, keys to species were not common in floras and only rarely seen in revisionary studies. One of the innovations in the three-volume *An Illustrated Flora of the Northern United States, Canada and the British Possessions* by Britton and Brown was the use of indented, dichotomous keys to the species. The idea was probably adopted from the Berlin-based taxonomists who routinely provided keys to species in their works. The innovation was immediately adopted by western authors. For example, keys are lacking in Coulter's *Flora of Western Texas*, published in 1891, in Frederick V. Coville's 1893 report on the *Botany of the Death Valley Expedition*, and in Thomas Jefferson Howell's *Flora of Northwest America* (1897). But Jepson, who replaced Greene at Berkeley in 1895, included keys in his suite of studies on the plants of that state. In the 1901 *A Flora of Western Middle California*, Jepson indicated that his keys to family, genera, species, and in some instances even varieties, were designed to "apply only to the species listed" and that—as many can appreciate today—he had spent a "very great amount of time and effort" on their construction. He maintained the same degree of care in his other efforts: *A California Flora* (1909) and his condensed treatment *A Manual of the Flowering Plants of California* (1923). Jepson was as aware of the student market as Gray, Woods, or Britton. In 1902 he published *A School Flora for the Pacific Coast*. My first taxonomic work was Jepson's *A High School Flora for California*, which I used as a freshman at Sonora Union High School in 1955, 30 years after its initial publication.

One of the major evolutionary changes in floristic design that may be attributed to Jepson was the monographic style he developed for his *A California Flora* series. Like Gray before him, and his contemporaries Britton and Fernald, Jepson examined type material and wrote extended comments about each species. While on Jepson, it should be mentioned that he started the *University of California Publications in Botany* in 1902, which was an institutional journal, and was the first editor of *Madroño*, the journal of the California Botanical Club; it was first published in 1916.

LeRoy Abrams, who arrived at Stanford University in 1902, published a *Flora of Los Angeles and Vicinity* in 1910 in cooperation with the New York Botanical Garden, and in competition with Jepson, published the first volume of his *Illustrated Flora of the Pacific States* in 1923. Abrams adopted the illustrated flora format of Britton and Brown. Like them he included synonymy and provided each species with a common name. Unlike his eastern counterparts in this regard, Abrams fabricated the names; Britton and Brown had evidence for their use.

The Smithsonian Institution began its western campaign by publishing a series of local and state floras in the *Contributions*. The *Flora of the State of Washington* by Piper appeared in 1906, and Elmer O. Wooton and Paul C. Standley published their *A Flora of New Mexico* in 1915. A decade later, Ivar Tidestrom's *Flora of Nevada and Utah*

was published. The format of each book was a series of descriptive keys with distribution and ecological data added in an adjacent section. The detailed descriptive format of the Harvard- and New York-based floras was deleted. By the 1930s, this was the trend in most federally supported flora projects such as Kearney and Peebles's 1942 *Flowering Plants and Ferns of Arizona*.

The New York Botanical Garden was also extending its influence into the West. Rydberg's *Flora of Colorado* was traditional in format, but following the lead of his colleague John Kunkel Small, who was engaged in floristic studies in the southeastern United States, Rydberg later adopted a concise floristic style in his 1917 *Flora of the Rocky Mountains and Adjacent Plains* and his 1932 posthumously published *Flora of the Prairies and Plains of Central North America*. These works, with their precise keys and sparse but detailed descriptions, became the model that many others have copied.

The first modern manual was Fernald's *Gray's Manual of Botany*, published in 1950. It was carefully written, with detailed descriptions and excellent distribution and habitat data given for each species. In the descriptions, Fernald highlighted the diagnostic features of each species in italics. *A California Flora*, published by Philip A. Munz in 1959, also had excellent descriptions and distribution data. While Fernald illustrated an occasional species, Munz illustrated each family. The model developed by Munz was adopted by Correll and Marshall C. Johnston in their *Manual of the Vascular Plants of Texas*, published in 1970.

When the Pacific Northwest and Intermountain West floras were in their early planning stages in the 1950s under the influence of the New York Botanical Garden, Arthur Cronquist and C. Leo Hitchcock decided to merge various flora designs into two publications. The first was to be a multivolume, large-format, illustrated, monographic work with room for ample discussion. The second was to be a concise one-volume manual. The five-volume *Vascular Plants of the Pacific Northwest* was published from 1955 to 1969, with the one-volume *Flora of the Pacific Northwest* appearing in 1973. The latter work followed the expanded key-format of the Smithsonian-based series, but added illustrations along the margin of each page.

The first volume of the *Intermountain Flora* was published in 1972 with an expanded introduction. This format is being followed in the new multivolumed flora of North America north of Mexico.

As might be expected, as newer models for floras evolved in the West, they were later adopted by writers in the East. Strausbaugh and Core began publishing their illustrated *Flora of West Virginia* in 1952. The *Manual of the Vascular Plants of the Carolinas*, by Radford, Ahles, and Bell appeared in 1968; it included distribution maps. The two-volume work on the vascular plants of Maryland by Russell G. Brown and Melvin L. Brown used color photographs and line drawings. They also annotated their illustrations so that in many instances it is possible to key out a plant merely by examining the figures. The *Flora of the Great Plains* is a two-volume work, with one dedicated to distribution maps and the second a descriptive manual modeled after those written in California and Texas. Two excellent Midwest floras are being published currently: *The Illustrated Flora of Illinois* by Robert Mohlenbrock and *Michigan Flora* by Edward Voss. These are monographic in style, but the books are of a smaller size so that it will require several volumes to complete the work.

Specialized manuals rapidly came into being as well as the more general flora. While illustrated silvas were common, dating back to those by F. A. Michaux (1841–1842) and Nuttall (1842–1849), Charles Sprague Sargent's *The Silva of North America*, published from 1890 to 1902, is the best known. Other specialized manuals were published as well: the *Manual of the Grasses of the United States* by A. S. Hitchcock first appeared in 1935, with a revision by Agnes Chase released in 1952. *A Manual of Aquatic Plants* was published by Norman C. Fassett in 1940 and in a revised edition by Eugene C. Ogden in 1957. This illustrated manual led to Mason's *A Flora of the Marshes of California* in 1957, which led to *Aquatic and Wetland Plants of Southwestern United States* by Donovan S. Correll and Helen Correll in 1972. The latter was followed by a companion work for the southeastern United States by Robert K. Godfrey and Jean W. Wooten in 1981. Kenneth K. Mackenzie's 1940 *North American Cariceae* is reminiscent of the kind of illustrated works published in the 1700s in Europe.

The increased popularity of wildflower books with fine illustrations or photographs evolved into informative works on American trees, mosses and bryophytes, fungi, lichens, and algae. One of the first western books was *The Wild Flowers of California* written by William Doxey and published in 1897. Harold W. Rickett's series of books published from 1966 to 1973 on the wildflowers of the United States with its elegant colored photographs has become a classic of its kind. The same may be said of Carlyle A. Luer's two volumes on

the orchids of the United States and Canada published in 1972 and 1975. The scholarly *A Field Manual of the Ferns & Fern-allies of the United States*, published in 1985 by David Lellinger, is illustrated by a series of excellent color photographs taken by A. Murray Evans.

Numerous checklists and local florulas have been published for portions of many states, especially in western America. John Thomas Howell in California and Stanley L. Welsh in Utah have authored or assisted in many such publications. Recent works have been published for Louisiana and other states in the Deep South.

Two trends have evolved over the past 30 years. First, many manuals are so expensive that some—notably the 1980 *A Flora of New Mexico* by William C. Martin and Charles R. Hutchins, and Robert D. Dorn's 1977 *Manual of the Vascular Plants of Wyoming*—are hardly used. Second, regional floras now have multiple authors, and even those for states or portions of states often have several contributors. While multiauthored works often result in highly variable taxonomic treatments between groups, there is often a greater consistency between publications because the same specialist is invited to contribute treatments for several works. The *Manual of the Vascular Plants of Texas* was one of the first multiauthored volumes in the modern era, although the unfinished *Contributions Toward a Flora of Nevada*, begun in the 1940s, was earlier. This trend will reach its pinnacle in the revision of Jepson's *Manual* for California and in the new national flora for North America north of Mexico.

The Evolution of Botanical Institutions and the Frontier Hypothesis

The evolution of institutions on the frontier was, like that for explorations, time-related and influenced by developments in adjacent regions of settlement. The first scientific societies began in 1660, but such modern institutions as the British Museum were not established until 1753. Governmentally supported research in Britain began in the 1770s and gradually replaced that which had been privately funded in the past. In the eastern United States, individuals with modest libraries and collections were not uncommon in the formative years of the nation, but few could afford to send out major expeditions. Thus, the federal government, rather than a group of individuals, a society, or an institution, sponsored the Lewis and Clark expedition.

Few specimens gathered in temperate eastern North America remained in the New World. The majority went to England and France where they were incorporated into private and public collections. When specimens did remain, they were too often lost or destroyed. The first set of John Clayton's Virginia plants, his Ehret drawings, and his library and manuscripts were burned by the British during the Revolutionary War. Still, the herbarium of Stephen Elliott at The Charleston Museum, established in 1773, has managed to survive.

The privately held collections of Henry Muhlenberg, William Barton, and others in the Philadelphia area formed the nucleus of the Academy of Natural Sciences, which was established in 1812. Many private collections were eventually housed at universities along the Atlantic seaboard, with Harvard, Yale, Columbia, and Princeton having major herbaria early in their histories. The Gray Herbarium at Harvard University, formally established in 1864, had a long prior history thanks to the efforts of Nuttall, Gray, and others. Even the herbarium at the Smithsonian Institution was active before its formal date of establishment in 1868.

The tradition eastern institutions inherited from Europe was one dominated by influential men in positions of power. Prior to 1776, most of those in power in Europe were also wealthy. In the United States, a monied class did not exist so that institutional power came from a combination of position and education. By the 1830s and 1840s, when Torrey and Gray dominated systematic botany, European institutions had evolved to the point that talent too was more important than wealth. Britain's Bentham and Hooker were not poor in any sense of the term, but both were sufficiently talented to dominate taxonomy regardless of their individual monetary worth.

In the United States, as systematic institutions began to form nearer the western frontier, Torrey and Gray dominated the field and virtually controlled all who collected and published. They chose who was appointed to government-sponsored expeditions, and not surprisingly, saw to it that all of the collections generally went to them for identification and publication. When Kellogg and his associates established the California Academy of Sciences in 1853, and Englemann and Shaw joined forces to form the Missouri Botanical Garden in 1859, their activities were blessed by Gray.

Systematic institutions in the United States gradually became fragmented with the establishment of competing government, museum, and university herbaria. Because museums were found primarily on the East Coast, university herbaria (with the exception of Harvard) there generally failed to

become major centers of power. Even when the systematic community began to fragment regionally, no university herbaria in the East was able to dominate floristic and systematic research to the extent that the Smithsonian, Harvard University, and the New York Botanical Garden had done.

In the Midwest, university and museum herbaria, more isolated but not totally divorced from their eastern counterparts, began to expand their circles of influence so that they could produce significant regional floras, but these efforts were minimal until the 1960s. On the Pacific Coast, university herbaria competed directly with local museums and botanical gardens for support, adjusted with them to the changing requirements of systematics, and yet often failed to cooperate. Still, one survival strategy was for university herbaria to concentrate on monographic research, with museums and botanical gardens devoting their resources to floristics.

The regional sectionalism that resulted after Gray's death in 1888 was exacerbated by the institutional infighting between Harvard and the Smithsonian Institution over the demand by the Smithsonian for the return of collections made on federally supported western expeditions. With the increased independence of western botanists, the sudden growth and the attempted domination of the eastern elite by the New York Botanical Garden caused additional bitterness. This came in the form of New York's rapid domination of floristic regions previously considered to belong to Harvard or the Smithsonian. To protect its interests, each institution made further demands upon universities, taxonomists, and editors for allegiance and support for their particular points of view.

The development of class and regional sectionalism are natural stages in the evolution of institutions. Like the individuals at them, there was a concomitant increase in conservative views, with occasional attempts by the major institutions to dominate, or at least control, the ideas and concepts that were evolving on or near the frontier. The small western institutions argued that the eastern establishment was attempting to control floristic studies at the state and regional level. Yet these institutions had the collections, libraries, and type material to do the work. They also had the talented scientists with the time and funding to accomplish the tasks. While local florulas were left to the state universities, most western floras were worked on with the permission of or in concert with a major eastern institution.

By 1889 the so-called eastern establishment had expanded to include the California Academy of Sciences and the Missouri Botanical Garden, with a few universities, such as the University of California at Berkeley, assuming major leadership roles in systematic botany. Smaller institutions in the West were often under the direct influence of one of these larger institutions, and good working relationships between them were common. For individual western collectors the truce was anything but smooth, yet most became associated with one of the establishment institutions. Greene, a festering sore in Gray's side, went to the California Academy, then Berkeley, and finally to Washington, D.C., where he used the facilities of the Smithsonian. Jones worked as a collector for the federal government and identified his collections at the Smithsonian. He also published initially in journals controlled by the Academy and by Jepson. Heller, isolated at the University of Nevada, collected for the federal government, then for the Academy, and finally for the New York Botanical Garden.

In each instance, the lure of a larger institution was overwhelming even to the most argumentative of the independent naturalists.

Specimen exchange programs soon developed among most of the institutions, with the majority of specimens moving from the smaller herbaria to the larger ones. As the frontier moved westward, those near the edge gradually became the favored repository of the local collectors because by then they had enough of a library and herbarium to serve their needs. Large herbaria soon developed at most of the land-grant universities. Herbaria at the University of Washington (1880), the Rocky Mountain Herbarium at the University of Wyoming (1889), the University of Arizona Herbarium (1891), and the herbarium at the University of Texas (1900) were quick to grow and dominate floristic and monographic research efforts in their respective regions.

Unlike the general success of the major institutions to attract large collections and talented scientists, the success of the smaller ones was usually dependent upon the personality and ability of a single taxonomist. The growth and success of university herbaria such as the Intermountain Herbarium at Utah State University was due largely to the efforts of Maguire and Holmgren, its first two curators. Likewise, the enormous growth of the herbarium at Brigham Young University since 1965 can be credited to Welsh.

Throughout the West there was a step-like evolution of people and institutions as the floristic wilderness disappeared. General collectors were replaced by more regional collectors who were then replaced by monographers. As taxonomy became

more sophisticated, the monographers were replaced by experimentalists so that now, at least in many universities, few systematists are knowledgeable of even the local flora.

Even the teaching of systematics has changed. In the past students were first introduced to the regional flora, often writing a master's thesis of a particular area. Once having gained first-hand experience with several groups of plants and the cognate literature, the student went on for a doctoral degree specializing on a genus. This changed in the 1960s and 1970s, so that now few students are familiar with any local flora, and many have little experience beyond the species level because most do their doctoral research only on a portion of a genus. Likewise, many students today have only a limited knowledge of nomenclature, plant families, the botanical literature, and almost no sense of the past.

Nonetheless, modern innovations in systematics over the past 50 years have tended to come from the university community with its young and aggressive faculty and innovative students. Several have taken a leadership role in certain areas. One example was the development of chemosystematics by Ralph Alston and Billie Turner at the University of Texas. Leslie Gottlieb at the University of California at Davis did much to establish electrophoretic techniques as a useful tool in systematics, and Douglas Soltis, Christopher Haufler, and Gerald Gastony are all currently making fundamental contributions to the field at their home institutions.

The frontier hypothesis predicts that the established, more conservative institutions will periodically attempt to specialize and diverge from their established missions. In doing so, those with strong traditions for change will succeed as long as the specialization does not threaten the institutions' main missions. Many, however, will fail or at least wane and fall from prominence, with influence and power shifting to more dynamic institutions. The hypothesis states that such dynamic institutions will always be closer to the frontier.

Universities with large and diverse faculty in systematics tend to be successful in changing emphases and maintaining successful programs simply because of their size. Whether or not they retain their position in systematics depends to what extent they abandon their traditionally strong areas of research. Interestingly, where the systematics staff is small, the institution tends not to rid itself of the service aspects of its taxonomist; rather, it allows the other necessary academic disciplines, such as anatomy, cytology, morphology, and paleobotany, to fall aside, thereby preventing continuation of a viable graduate research program.

The national disappearance of botany departments and the demise of organismal biology on university campuses may seem to discount the above assertions. Still, many administrators realize that for an institution to become "modern," it must be at the expense of the classical fields, and thus it becomes a philosophical question whether their traditional mission should be fulfilled. To avoid this uncomfortable question, administrators tend to establish isolated "institutes" so as to divorce their researchers from the day-to-day routine of dealing with academic matters. Classical scientists are therefore retained in teaching and service positions with limited in-house funding—well isolated from the activities of those who are considered to be doing real science. This results in internal sectionalism, which is often coupled with profound personal bitterness among the individuals.

Mature museums and botanical gardens, in an effort to be on the cutting edge in research, often fail in their community responsibility of being a primary resource center. When they attempt to follow fads, and available research dollars, by hiring narrowly trained specialists in peripheral, often exotic fields, it is typically done at the expense of those people who are familiar with plants and whole floristic regions of the world. The newly hired curators, to remain competitive, cannot afford to be interested in collections, exchange programs, or large-scale fieldwork. As a result, the primary mission of the institution is not fulfilled, to the distress of others who depend upon its accumulated resources. For those who remain, there is a lessening of available funding as the institution fails to attract the research dollars needed to operate its exotic programs, and with fewer broadly trained staff, it can no longer maintain its position of importance. This often results in internal classism with accusations and condemnations that can only hasten the demise of the institution.

The underlying force behind all of these predictable trends, according to the frontier hypothesis, is the lack of a near frontier. Researchers once interested in the wilderness flora of temperate North America are now working in the tropics, where there is still a substantial floristic frontier. Institutional interests at all levels, but particularly those in the larger national and regional museums, botanical gardens, and universities, have always been on the frontier, and today that means the tropics. Funding agencies, and those few systematists who control the dispersal of research funding,

are often guilty of concentrating available funding on the latest fad, arguing that this is the only way they can justify their budgets to the administration and to Congress. The disquieting trend, and the one that must be fought, is the tendency with maturity to assume that the work done on the old frontier should end simply because the excitement and challenge of the frontier are gone.

Beyond the American Floristic Frontier

What is the future of systematic botany in temperate North America, especially in the continental United States, now that there is no longer an unknown wilderness beyond a floristic frontier? According to the frontier hypothesis, we can expect a consolidation of institutions and a reduction in their numbers. We can expect a greater conservativeness to envelop the field, especially as it relates to nomenclature and other aspects of classical taxonomy, including floristics. While the natural evolution of technology will continue to be exploited, its application will be restricted to fewer individuals and fewer institutions. Furthermore, the half-life of any new fad will shrink, with most contributing little to our broad understanding of evolution and systematics.

These trends are predictable and will come to pass. Policies to prevent them will not succeed and generally will not be attempted. The problem to be addressed by those who work on the temperate flora is how do we proceed? Predictably, we must consolidate our research efforts, reduce our expectations, and sacrifice knowledge on the biology and natural history of all our plants in favor of being permitted to evaluate a few.

In short, to work on the plants of this newly settled region we must do precisely what the frontier hypothesis says we will, even with the predicted adverse consequences.

Sectionalism will increase, exacerbated by the haves and have-nots. Instead of the kind of sectionalism now found, it will evolve into one involving national versus international interests. Large, multi-institutional international projects will dominate systematics at the expense of individual scientists examining a single group of plants. Even monographic work will change, with funding going primarily to those who put together a team of scientists to accomplish what one, in the past, could have done just as well at far less expense. Still, with the demise of the classical "herbarium taxonomist," there will be such a profound loss of knowledge that it will take years to recover that traditionally inherited "institutional" knowledge of the plant kingdom so many have been able to learn simply by having a willingness to work and listen.

The frontier hypothesis predicts many of the best and brightest will continue to work on and beyond the floristic frontier wherever it exists. Funding in the future, as in the past, will continue to go preferentially to projects on the frontier. And technology will continue to drive the funding.

On the international level, the American systematic community must remember that while the United States no longer has a floristic frontier, other nations in the Americas do. We must be willing to address the concerns and needs of those still on the frontier. Much as we resented the exploitation of our wilderness flora by the Europeans in the past, so too do those on the frontier resent exploitation by American systematists today. We have done much to address the concerns of others; yet, we must do more and to do so will be costly. That means an effective transfer of funds, people, and knowledge must occur.

We must also be aware that the amount of time for each evolutionary stage to occur on the remaining frontiers will be much faster in the future. It took some three centuries for the floristic frontier to move to the base of the Rocky Mountains and the Sierra Nevada, but only one to eliminate the remainder of the wilderness across the Great Basin of the American West. With the rapid, exploitative destruction of the tropics, we have little time to make even the most basic observations on the native vegetation before it will be so altered that its significance will be lost forever. Therefore, a degree of urgency does exist—which did not exist in 1889—and if we are to gain any useful knowledge of the plants found in many of the world's last remaining wildernesses, we must act as any adventuresome taxonomist would: head for the frontier! That is where the challenge is; that is where the research dollar is.

Conclusion

In this symposium we have commemorated a century of botany, 1889–1989. The changes that have occurred over the century since Turner proclaimed the close of the American frontier have been great. A maturation of people, institutions, customs, and traditions is predicted by the frontier hypothesis. We should continue to improve well into the future as long as systematists and systematic institutions do not become so rigid that they cannot change with the times.

The past century of botanical exploration has brought us to the point in our evolution that, like this nation a century ago, we too are in a position to expand and mature. We do not yet need to fear rigidity, but we do need to be cautious. Indeed, we will experience advances similar to those of the nation since 1890, but in a much shorter period of time. If our future is not to be dim, we must be alert. How we direct our future, and how much we are willing to invest in the maturation of our nation's floristic and systematic community, must be something we decide. To leave it to a few, or worse yet, to outsiders, means that we are forgetting one of the most important lessons of the frontier: to be free is to have liberty, and to have liberty means we must participate in the processes that give it a voice.

THE NIGER AND THE NILE: BOTANICAL EXPLORATION AROUND TWO AFRICAN RIVERS

F. Nigel Hepper[1]

ABSTRACT

Knowledge of the plants of Africa has been obtained by exploration and taxonomic study. While west Africa is dominated by the River Niger, northeast Africa has the famous Nile, with its major branches of the White and Blue Niles. This paper outlines more than two centuries of botanical exploration by individuals and organizations in these regions, relating them to the colonial and governmental history of each period, and links the value of the knowledge gained to the environmental concerns of today.

The Niger and the Nile—the two great rivers of Africa north of the equator—lie to the west and east of the continent. For centuries even geographers thought that the Niger flowed out through Senegal, owing to the hidden nature of the Niger's debouchment with the Atlantic Ocean via a multitude of outlets in Nigeria; they also thought the Niger and the Nile had a common source in the Mountains of the Moon (Senex, 1721). The real source of the Nile, however, was a mid-eighteenth century objective as much sought after as a moon landing was in the mid-twentieth century.

If we look back on the past century we see that this time span encloses most of Africa's colonial period. Before the 1880s only a few, scattered European trading posts located along rivers, such as the Niger and Senegal, could be reached by ship. This situation was altered by the "scramble for Africa," starting with the Berlin West Africa Conference of 1884–1885, when European imperial powers scrambled to gain colonial possessions. By 1898 all of Africa except for Liberia and Abyssinia was carved up into colonies (see Fig. 1). Less than three-score-years-and-ten later, however, the colonies were becoming independent nations. Gold Coast became Ghana in 1957, and in quick succession other British and French possessions gained nationhood, with only Portuguese territories resisting until the 1970s.

Botanical exploration adapted to these changing conditions, and it is no accident that the main African herbaria were established in the imperial cities of London, Paris, Berlin, Brussels, and Lisbon, which were the capitals of Britain, France, Germany and Portugal, the states that controlled their African colonies.

PRELIMINARY EXPLORATIONS

Ever since the time of Henry the Navigator (1345–1460), when the Portuguese in the fifteenth century sent their caravels to explore coastal regions ever further around Africa, European nations sought the spices of the Far East, rather than conquest of unhealthy tropical Africa itself. Not until the eighteenth century were herbarium collections and serious botanical observations made. The first were the French, with Adanson in Senegal (in 1749–1754), and Palisot de Beauvois (in 1790) in Oware and Benin, which are now parts of Nigeria (Aubréville, 1962). The British Duchess of Portland sent the Dane Henry Smeathman to Sierra Leone to settle released slaves in 1771; William Brass was sent by Kew's Sir Joseph Banks to the Gold Coast in 1780 (although Keay [1962] stated that Brass actually collected more gold than plants). The Danes were early seafarers who established forts on Africa's west coast. It was from Christiansborg Castle in present-day Ghana that P. E. Isert and Peter Thonning made their important plant collections between 1783 and 1803. They set out to find medicinal herbs and to help the Africans create better farms to alleviate their poverty (Hepper, 1976, 1979a).

Virtually nothing was known of the natural history of northeast Africa until the second half of the eighteenth century (see Fig. 2). Two notable expeditions dramatically opened up the flora and

[1] The Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE.

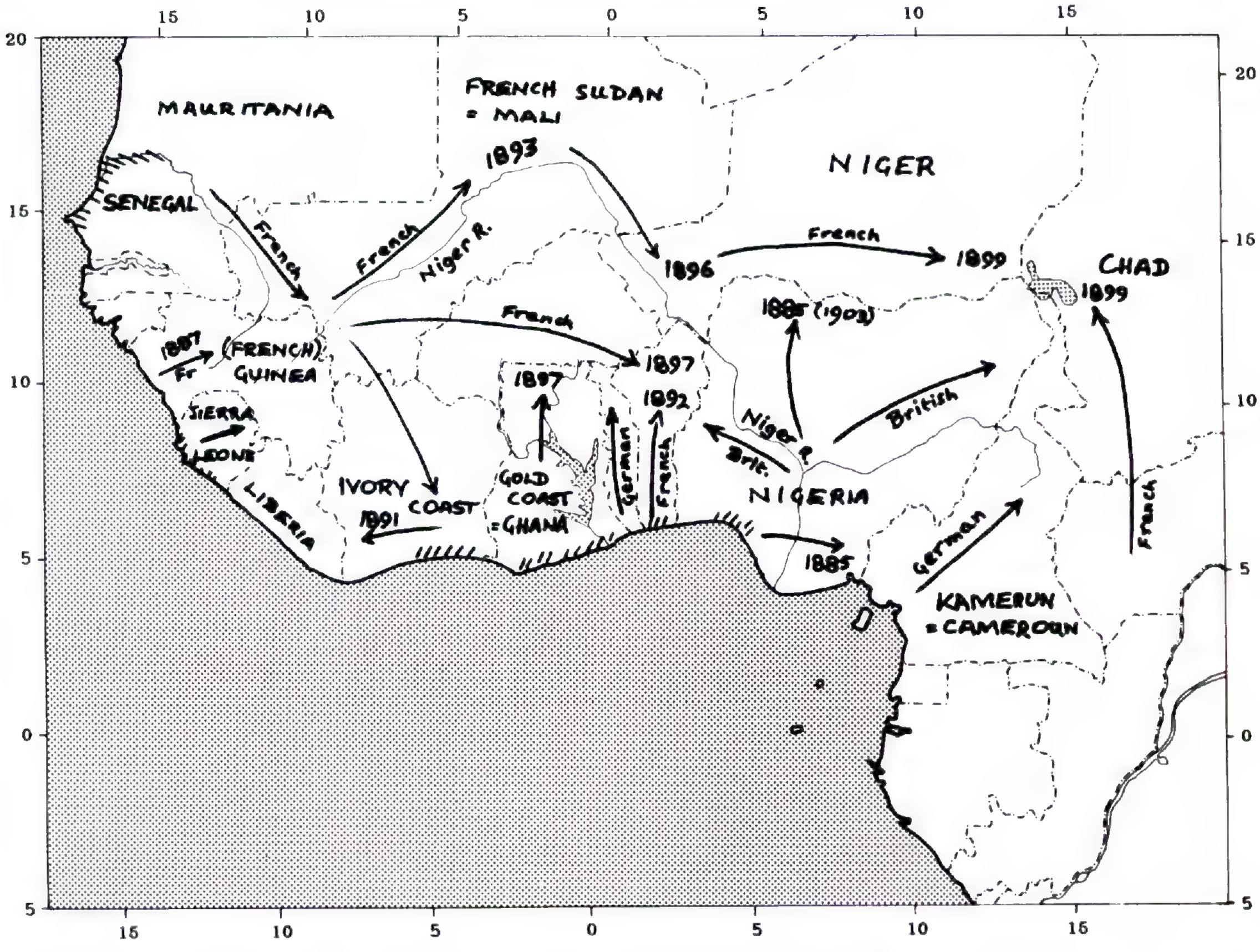

FIGURE 1. The Niger and West African colonization. (Based on J. Fage, 1978, *An Atlas of African History*, Edward Arnold, London.)

fauna by approaching the region along the Egyptian Nile and the Red Sea. The first was a royal Danish expedition with the botanist Peter Forsskal, who died in the Yemen in 1763. (I include this because many of the plants [and animals] he collected have an African distribution and affinity, rather than an Arabian one.) The sole survivor of this expedition, Carsten Niebuhr, sent back Forsskal's natural history collections to Copenhagen University. I am at present revising that important botanical material (Hepper, in prep.).

The other expedition was led by James Bruce to Abyssinia (now Ethiopia), which he reached in 1770 and about which he published his five-volume *Travels* (1790). This work included illustrations of 15 species of plants (the second edition of 1805 increased the number to 27), as well as engravings of some birds, mammals, and other creatures. Much has been written about this expedition to discover the source of the [Blue] Nile (Head, 1836; Moorehead, 1962), but little has been known about his companion Luigi Balugani. This Italian artist, who died in Gondar in 1772, had drawn more than 150 plants and many animals during this African expedition, some as superb finished water colors. Most had been overlooked until I worked on them at the Yale Center for British Art and realized that when Balugani drew them they were new species that remained unknown until later explorers collected them. At last Balugani takes his place, according to Paul Hulton, formerly of the British Museum, as a major eighteenth-century artist alongside John Parkinson of James Cook's voyage (Hulton et al., 1990).

THE FIRST HALF OF THE NINETEENTH CENTURY

Napoleon's savants in Egypt included the botanist Delile (1809); further up the Nile, Bruce and Balugani were followed by Henry Salt (1832–1833) and more importantly by others including Quartin-Dillion and Petit in the 1830s, and the German W. P. Schimper, who lived in Abyssinia from 1837–1878 and who made large and important collections of plants. The Sudan was visited mainly by French (F. Caillaud in 1819–1822) and Italian (G. Raddi in 1827–1829) explorers (Cufodontis, 1962).

In West Africa, the early nineteenth century saw increasing numbers of expeditions, partly for

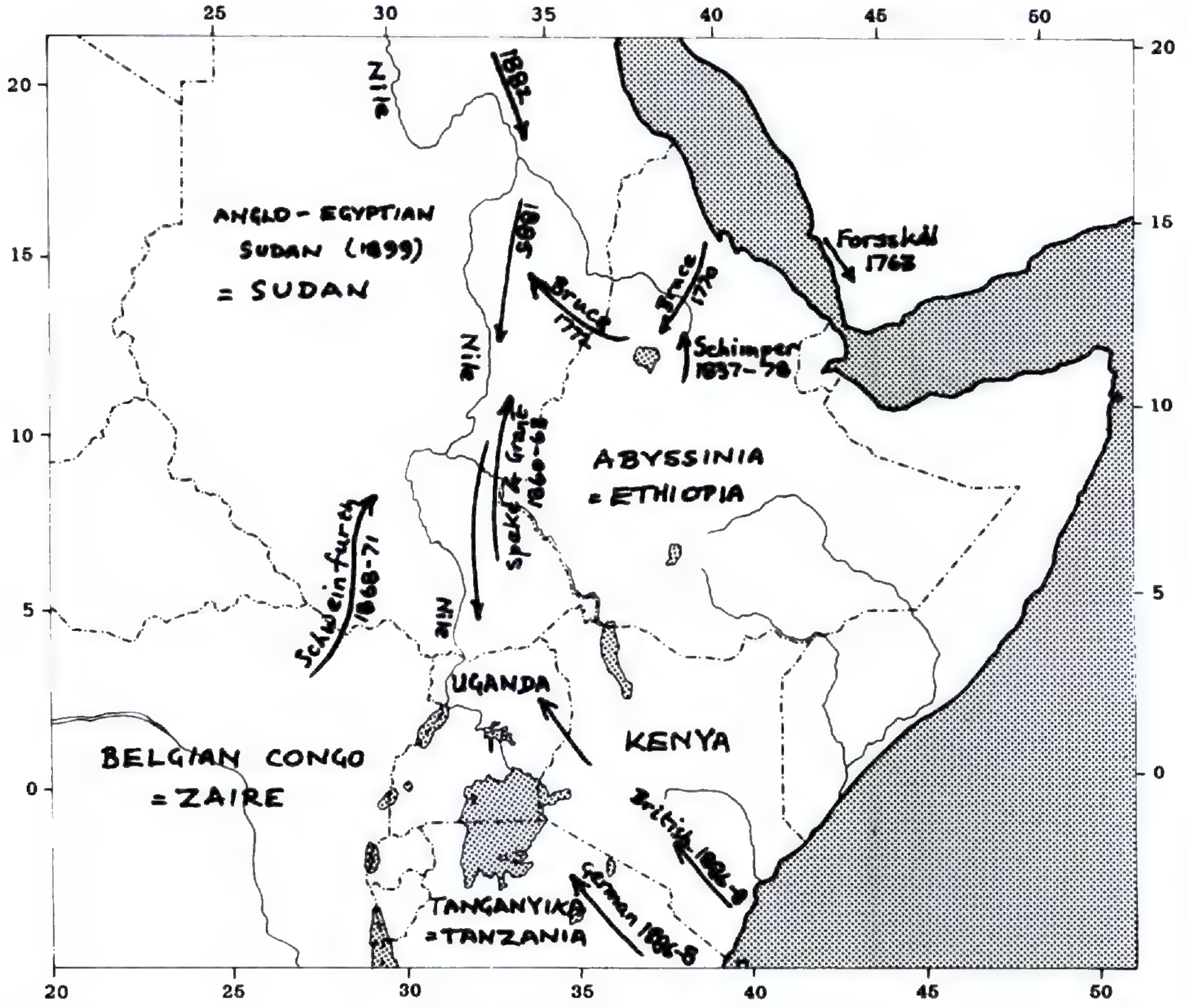

FIGURE 2. The Nile and East Africa. See text for explanation.

trading purposes and partly to resist the Portuguese slave trade; along on the ships went naturalists. In the 1820s and 1830s the French sent the botanists Perrottet, Leprieur, Richard, and Heudelot to Senegal, and their herbarium material was received at Paris. The British explorers, such as Mungo Park, who perished in the Niger in 1805, and Clapperton, who reached the Niger from the coast in 1826, collected few plants. An ill-fated expedition to the Niger in 1841 lost most of its crew because of disease. The botanist Theodor Vogel also succumbed, although he had collected many plants that found their way to Kew. Fortunately, the next expedition under Dr. W. B. Baikie in 1854 was equipped with quinine, which successfully controlled malaria. During Baikie's return visit to the Niger in 1857, however, his ship "Dayspring" wrecked at the Jebba rapids, and Charles Barter's herbarium collection was lost. Undaunted, Barter made friends with local chiefs and collected another 2,000 specimens in the vicinity while waiting for a replacement ship. He did not survive the two years required, however, and was in turn replaced by another Kew botanist, Gustav Mann (Hepper & Neate, 1971).

THE "HEROIC PERIOD" OF AFRICAN EXPLORATION

According to Gillett (1962), the "heroic period" extended in East Africa between 1860 and 1888, with famous expeditions such as those by Speke and Grant and the German explorations to Mt. Kilimanjaro led by Decken. Here I overextend my terms of "the Nile area" in East Africa. The 1886 Anglo-German agreement decided the spheres of influence of the trading companies, and the direct imperial administrations created the period of colonial establishment between 1888 and 1918 (Gillett, 1962). The British areas of Uganda and Kenya included the headwaters of the Nile at Lake Albert, while Lake Victoria impinged on German Tanganyika (see Fig. 2). Meanwhile in the north, following the British occupation of Egypt in 1882 and the Mahdist revolt in Sudan 1881–1898 (during which occurred the death of General C. G. Gordon in 1885), the joint Anglo-Egyptian Sudan was set up in 1899. This opened up the entire Nile to exploration, although in 1863 Samuel Baker had almost reached Unyoro (now Bunyoro in Uganda), and in the opposite direction Speke and Grant arrived at

Khartoum in 1863. Georg Schweinfurth's epic journey from Congo to Egypt (1866–1872) yielded a large collection for Berlin (Cufodontis, 1962; Gillett, 1962).

In between the Nile and the Niger, the French conquest of the Lake Chad region and the Shari and Ubangi river basins by Lamy and Archambault in 1899 linked equatorial Africa with French West Africa, but the Germans took Kamerun (Cameroon) eastward of British Nigeria. C. Ledermann was the botanist on the German Adamaua expedition through Cameroon from 1908 to 1909, during which he collected 6,492 plants. Unfortunately, few duplicates were distributed and most were later destroyed in Berlin during World War II (Hepper, 1974). Fortunately, many of G. W. J. Mildbraed's Cameroon collections are represented in other major herbaria and were included in Letouzey's (1963) *Flore du Cameroun*, which itself has provided an incentive for further biological exploration.

Nigeria had seen an amalgamation of trading companies in 1879; by 1897 Nigeria was taken somewhat reluctantly under the British crown, and military expeditions pushed north to Sokoto declaring it a Protectorate. In the meantime (1879–1893), the French military had made rapid advances from Senegal eastward through the Sudan country under the asssumption that the most advanced and productive parts of West Africa lay there. Thus, the British and French forces met, and defining territorial limits was necessary to avoid disputes. It was during boundary commissions, such as that between Sierra Leone and French Guinea (1891–1892) on which G. F. Scott-Elliot was able to collect plants for Kew, that serious botanical investigations took place.

In the 1860s the director of the Royal Botanic Gardens at Kew, Sir William Hooker, had initiated the plan for the *Flora of Tropical Africa* as one of the proposed series of colonial floras detailing the plant life and potential products of the British Empire. With hindsight one cannot help but be amazed that such an undertaking was started when so little was known about the interior of Africa, yet it was a significant work that continued until 1937. The preparation of this 11-volume work must have stimulated botanical exploration and the collection of herbarium material, as did the first edition of the *Flora of West Tropical Africa* by J. Hutchinson & J. M. Dalziel during the 1920s and 1930s.

First Half of the Twentieth Century

By the twentieth century in both West and East Africa botanical studies began to be made by residents based in departments or offices. In 1908, H. N. "Timber" Thompson founded the Gold Coast Forest Department and soon afterward became superintendent of forests at Lagos (W. Nigeria), where he designated forest reserves. In 1892, the Germans established a botanical garden on the Cameroon coast at Victoria where Dr. P. R. Preuss studied the flora; in Tanganyika in 1902 the Germans founded a herbarium at Amani (which much later was transferred to Nairobi's East African Herbarium). Botanical exploration of the Anglo-Egyptian Sudan for British Museum (Natural History) collections resulted in Andrew's *Flora* (1950–1956). In Egypt, the Swede Vivi Tackholm and her Egyptian colleague Mohamed Drar published four volumes of their *Flora of Egypt* (1941–1969), which was never completed.

From 1899 to the 1930s the notable and energetic Auguste Chevalier sponsored West African botany in the French territories, and he amassed a huge collection at the Paris herbarium. He was followed by another of similar stature, André Aubréville, who published much including an illustrated, three-volume *La Flore forestière de la Côte d'Ivoire* in 1936.

Second Half of the Twentieth Century

Since the Second World War, increasingly more African nationals have become involved in botanical exploration. Following the war, institutes of higher learning and research stations with herbaria were established and were linked by motorable roads. Roads had a counterproductive effect on plant collecting as well, as it became increasingly difficult to travel *off* the roads! Porters were expensive or unprocurable, and the scatter of rest houses about a day's walk apart fell into disuse in favor of hotels or lodges at wide intervals along the roads. On the positive side, resident government officers were able to settle down to extended study of large or small areas. Some notable collections have been made by amateurs, including wives of officials posted to out-of-the-way places—the best known is Mary Richards, who lived in Zambia outside our area of consideration. Others such as Mrs. Faulkner in Tanzania and Mrs. Tweedie in Kenya were good correspondents of Kew. Controlling governments, and later aid donors, sent missions to regions to report on the forestry, pasturage, geology, and so forth, which resulted in large collections of often, regrettably, inadequate specimens. Local herbaria were active in identifying material, usually in cooperation with Kew or Paris. Thus in Sierra Leone, F. C. Deighton's study of pathogenetic fungi resulted in the formation of

an excellent agricultural herbarium at Njala. In Ghana the Forestry Herbarium at Kumasi was under the erudite, self-taught A. A. Enti, who transferred to the University of Ghana and there built up a much larger and active herbarium under C. D. Adams, J. K. Morton, and J. B. Hall. In Nigeria the largest herbarium is still at the Department of Forest Research in Ibadan, which was very active under R. W. J. Keay, who helped prepare *Nigerian Trees* (1960–1964). As well as collections by resident botanists, exploration by visitors continued for general collections like my own to remote parts of northern Nigeria (1957–1958) and from Senegal to Lake Chad by hovercraft along the River Niger (1969) for the revised edition of the *Flora of West Tropical Africa*. Specialist collecting gradually increased again with fine work by F. White (Ebenaceae); D. J. Mabberley of Oxford (mountain flora); O. Hedberg of Uppsala (mountain flora); R. M. Polhill of Kew (Loranthaceae); C. Grey-Wilson of Kew (*Impatiens*); B. L. Burtt of Edinburgh (Gesneriaceae); and many others. The Association of African Taxonomists (AETFAT) has done much to channel and coordinate such studies and explorations, and they have collaborated on publications such as their Index (Léonard, 1954–) and vegetation maps (Keay, 1959; White, 1983).

The tremendous burst of activity after independence from colonial rule was badly hit by the rise of oil prices in the 1970s, the slump in oil demand in the 1980s, and inflation generally. Foreign currency was unavailable for botanical journals and equipment, fuel, and even food. For example, in Nigeria and Ghana most activities were suspended for many years, yet J. B. Hall & M. Swaine (1981), with D. Abbiw's help, managed to make a study of Ghana's tropical forests that is probably the most comprehensive of any in the world. An active center in the Ivory Coast has continued under Professor L. Aké Assi. In Kenya, Christine Kabuye, following J. B. Gillett and colleagues, collaborated with Kew on the *Flora of Tropical East Africa* (Turrill et al., 1952–). Exploration of Ethiopia continued sporadically (Cufodontis, 1962), but the recent incentive by the founding of a flora project (Hedberg & Edwards, 1989) has meant concerted efforts by many international expeditions, unfortunately at a time when the vegetation is already decimated.

Future of the Environment

The present international awareness of and concern for the environment at last involves governments and donor organizations. They now begin to realize that tropical rainforests are crucial not only to the economy of African countries, but also to the well-being of the biosphere. Overseas aid is partly being directed toward conservation instead of development in the old sense—that of cutting down "the useless bush" in order to establish a plantation. Since the ancestors of the plantation crops occur in the bush, developers now realize that it is not useless after all. This gives added impetus to exploration of the vegetated habitats and the investigation of their constituent species.

Joint projects with zoologists, the World Wide Fund for Nature, and other donors in cooperation with national governments are concentrating exploration and research on special areas, for example, Gola Forest (Sierra Leone), Sapo National Park (Liberia), Tai Forest (Ivory Coast), Ankasa Forest (Ghana), Oban Forest (Nigeria), and Korup National Park (Cameroon). One project with which I have been concerned since its inception in 1986 is the Limbe Botanic Garden project for the conservation of genetic resources of associated rainforests on Cameroon Mountain. This project is supported financially by the British Overseas Development Administration and the Cameroon government and is linked with the Royal Botanic Gardens, Kew. It is refurbishing the old German garden at Victoria (now Limbe) as the administrative and research base for the species-rich forested areas (Hepper, 1989). Another project concerns the Missouri Botanical Garden. For more than a decade significant discoveries have been made by stationing plant collectors in strategic places, such as Korup in Cameroon where Duncan Thomas gained unrivalled knowledge of the flora and made many additional records. Other Missouri collectors elsewhere in Africa are making this herbarium America's major one for tropical African study. This may be the pattern for the future—international cooperation at various levels.

Concluding Remarks

Published maps (Léonard, 1965; Hepper, 1979b) show large gaps in the cover of botanical exploration in some African countries, such as Cameroon and Gabon. In Gabon, Breteler (1990) estimated that only 40,000 herbarium specimens have been collected thus far in a tropical forest covering a quarter of a million square hectares, and probably only 75% of the species are described. (Owing to general deforestation in Africa one may ask whether they will ever be known before they are destroyed.) By contrast, Ghana is now so well known that few additional species are likely to be found. Little is still known of the ecology or biology of most tropical species, and this is where future field

studies must concentrate (Hawthorne, 1990). Exploration of, say, the tree canopy to study epiphytes or the study of insect pollination may not be as hazardous a quest as the old Niger and Nile expeditions, yet we must find out what sustains plant life, or human life will be unsustainable on this planet.

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TICODENDRACEAE: A NEW FAMILY OF FLOWERING PLANTS

Jorge Gómez-Laurito[1] *and Luis D. Gómez P.*[2]

ABSTRACT

A new family is described to accommodate the genus *Ticodendron*. The unusual characters of this monotypic genus, with only *T. incognitum*, have been discussed by us elsewhere (Gómez-Laurito & Gómez P., 1989), analyzed by several experts in their special fields, and reported elsewhere in this issue of the *Annals*.

The discovery and description of new families of flowering plants is uncommon these days; only about 16 of a total 372 recognized by Cronquist (1981) were described since 1950. Many of the most recent new families, e.g., Alzateaceae (Graham, 1984) and Cecropiaceae (Berg, 1978), are taxonomic segregates of long-known entities. Others such as Saccifoliaceae (Maguire & Pires, 1978) and the most recent new family, Lacandoniaceae (Martínez & Ramos, 1989) were known almost from the beginning to be very close to long-established families (Gentianaceae and Triuridaceae, respectively). Such familiae novae as Tepuianthaceae (Maguire & Steyermark, 1981) and the new family described below for *Ticodendron* are rarer beasts, whose placement, even as to order, relies on detailed studies by numerous specialists looking at a variety of characters from wood anatomy to pollen ultrastructure. Results of these studies of *Ticodendron* are reported in a series of papers in this issue of the *Annals*.

Ticodendraceae Gómez-Laurito & Gómez P. fam. nov. Magnoliophytarum. TYPUS: *Ticodendron* Gómez-Laurito & Gómez P.

Arbor dioicus vel raro polygamodioicus. Ramulis teretis, cicatricibus teretis stipulorum delapsorum notatis. Stipulae subulatae, circundatae, caducae. Petiolis supra sulcatis. Foliae alternae; lamina elliptico-ovata, subcoriacea, margine in parte superiore serrata, nervis secundaris 8–13 paribus. Inflorescentia mascula 1.5–4 cm longa, simple ver ramificata, aliquando flos feminea coronata. Stamina numerosa, 2–4 verticillata disposita; bracteae 3 mox deciduae; filamenta 2–3 mm longa; antherae oblongae, 2 mm longae, basifixae; thecae geminatae, longitudinaliter dehiscentibus, conectivo subulato producto. Granulla pollinis triporata, minute spinulata, plerunque suboblata. Flos feminea solitariae extremitatis surcolorum dispositae. Bracteae 3, mox deciduae. Ovarium inferum in perianthum tubus inclusum, bicarpellatum, quadriloculare utroque loculo 1; placentatio axillis; ovula hemitropa, apicallis, pendula, crassinucellata, unitegumentata. Fructus drupaceus monospermus. Embryo oleosus, cotyledonibus rectus.

Dioecious or less commonly polygamodioecious trees. Twigs terete with the scar of stipules evident. Stipules subulate, encircling the stem, caducous. Petioles grooved above. Leaves alternate, blades elliptic-ovate, subcoriaceous, the margins serrate on the upper part, with 8–13 secondary veins. Male inflorescence 1.5–4 cm long, simple or branched, sometimes crowned by a solitary female flower. Stamens many, arranged in 2–4 verticels surrounded by 3 deciduous bracts, Filaments 2–3 mm long; anthers oblong, 2 mm long, geminate, attached by the base, the connective with an apiculate appendage, longitudinally dehiscent. Pollen triporate, minute spinulate, mostly suboblate. Female flowers solitary on pedicels, surrounded by 3 early-deciduous bracts. Ovary inferior, bicarpellate, included in the perianth tube, 4-locular with 1 ovule in each locule; ovules hemitropous on axile placenta, apical, pendulous, crassinucellate, unitegmic. Fruit drupelike, 1-seeded. Embryo oily with straight cotyledons.

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NEITHER OAK NOR ALDER, BUT NEARLY: THE HISTORY OF TICODENDRACEAE[1]

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Abstract

The newly described monotypic family Ticodendraceae is endemic to Mesoamerica, where it ranges from southern Mexico to central Panama. Although locally common in some areas very close to old collecting sites (at least in Costa Rica), few collections from prior to 1985 are known. Recent funds for exploration and concentration on the arborescent flora may account for the "rediscovery" of *Ticodendron* during the 1980s. It may also have been overlooked by botanists because it looks so familiar, like an oak or an alder. Most evidence suggests that it can be placed comfortably in the Fagales. *Ticodendron* is most common in the narrow strip of wet montane Atlantic slope forests between 750 and 1,500 m, where it often grows in association with endemic taxa of *Alfaroa*, *Oreomunnoa*, *Nyssa*, and other remnants of the Tertiary Laurasian flora. Further study and survey of this area will surely provide insight into the composition of that ancient flora surviving in Mesoamerica.

With the formal description of Ticodendraceae (Gómez- Laurito & Gómez P., 1991) in hand, this paper will present discussions of the history of discovery, distribution and habitat, biogeography, and a summary of relationships based on the following five papers, which present results of detailed studies of the wood anatomy (Carlquist), leaf anatomy (Hickey & Taylor), sieve-element characters (Behnke), floral anatomy and morphology (Tobe), and pollen morphology (Feuer).

History of Discovery

In one sense, when *Ticodendron incognitum* Gómez-Laurito & Gómez P. (1989) was described, its epithet could be taken as ironic. The recent history of this plant attests to the fact that many people knew a lot about it even before the species was formally published; correspondence among specialists during the years immediately preceding this compendium is measured in reams. We now know *Ticodendron* to have a rather wide distribution; as recently as 1984 it was known only from Costa Rica, but now is known to be locally common, from southern Mexico to central Panama. The plant is also quite well known to woodsmen; in Costa Rica alone it has at least four common names—two of them referring to it as a kind of alder (Gómez-Laurito & Gómez P., 1989). Yet, although *Ticodendron* was far from unknown at the time of publication, the Latin "incognitum" can have much the same meaning as the modern English usage of "incognito," and the fact that the family placement of this species has been such a puzzle makes the epithet appropriate. The plant has been famous in many ways, but its true identity has remained hidden (Fig. 1).

In spite of the fact that *Ticodendron* grows in relatively hospitable and accessible areas of moist to wet mid-elevation forests, some of which have been frequented by botanists for nearly a hundred years, we can cite only eight collections made prior to the 1980s. Four of those eight came to light recently, after the publication of the genus; *Ticodendron* has been hiding not only in the woods, but in the herbarium as well. Now that we know the tree we find it obvious and abundant, sometimes easily accessible at pasture edges and, at the right time of year, loaded with more or less conspicuous fruits (Fig. 2A) or littering the ground with the decaying fruits.

At first glance, especially when vegetative, this tree and its fallen leaves are easily mistaken for the common *Alnus* of the region, which often grows in the same areas as *Ticodendron* (Fig. 2B). One of the earliest known collections (*Lankester s.n.*, 1925), found recently by Aaron Goldberg at US, had been identified by an *Alnus* specialist as *A.*

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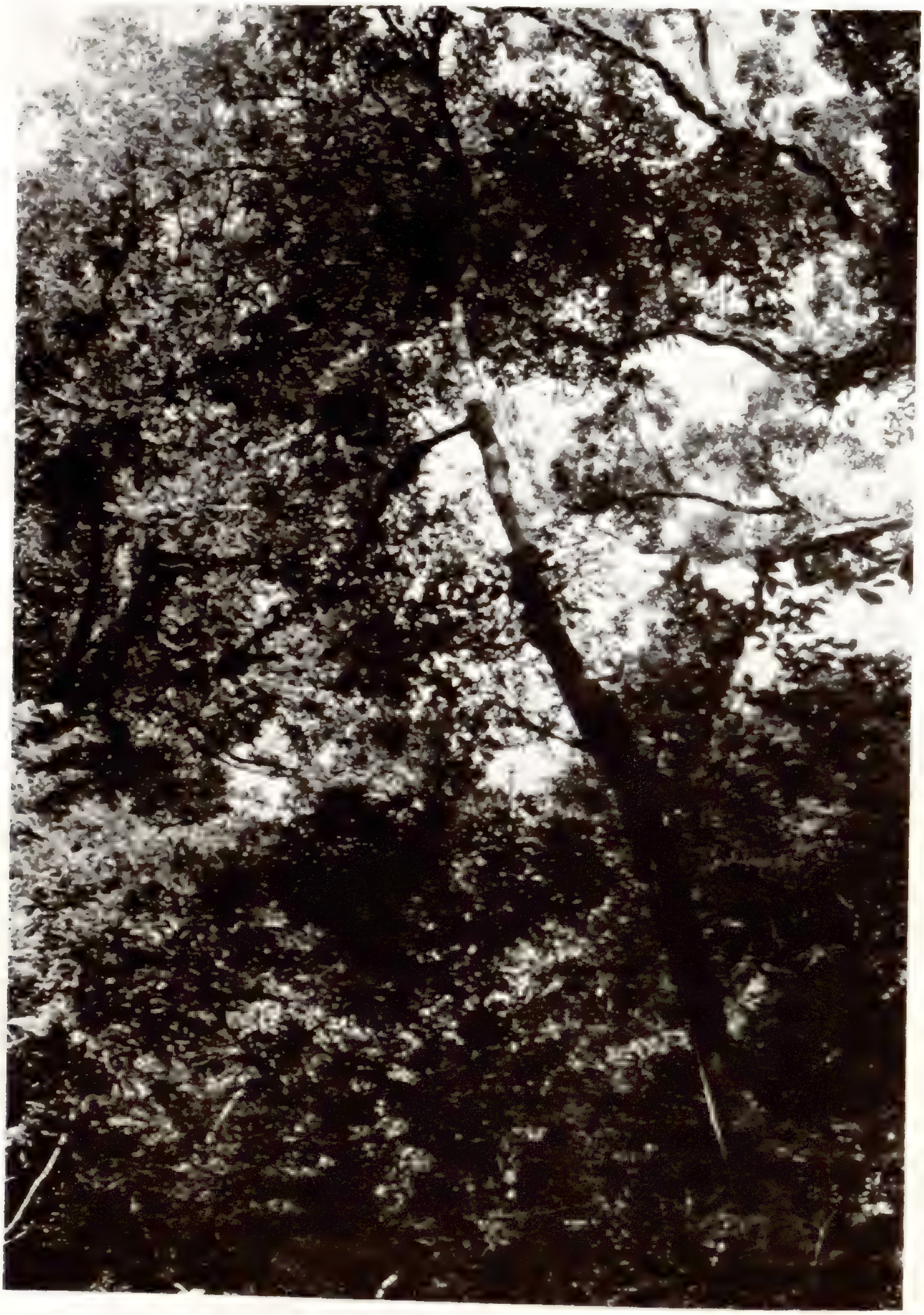

FIGURE 1. Mature tree of *Ticodendron incognitum* in forest at Monteverde, Costa Rica (*Gentry et al. 71474*).

acuminata subsp. *arguta*. Herbaria have scores of collections of *Alnus* from Central America, but why so few of *Ticodendron*? Why didn't industrious collectors like Brenes, Otón Jimenéz, Matuda, Pittier, Standley, Tonduz, or Williams collect it? Actually some of them may have; a recently rediscovered specimen at F with an early annotation "not Flacourt." made us take Steyermark off the above list at the last minute. Alternatively, why was this species not described by one of the early botanists who did collect it? It is conceivable that the species has been described, e.g., from sterile material, in a large genus, where no one thought to look.

The most likely reason that *Ticodendron* has gone so little collected and so long incognito is that it is most common in wet primary forest where intensive and persistent sampling of trees has begun only recently. Certainly trees are difficult to collect, and *Ticodendron* may have been overlooked for that reason. Also, the flowering period is apparently rather short and the flowers are inconspicuous. Many places accessible now by road were undoubtedly completely isolated 40 or 50 years ago.

FIGURE 2.—A. Fruiting specimen of *Ticodendron incognitum* (*Gentry et al. 71474*).—B. Young sapling of *Ticodendron incognitum* (*Hammel & Rivera 17834*).

Another answer might be conservativism. If good field botanists find fallen fruits beneath a tree with leaves that don't "fit" the fruits—i.e., because the fruits of *Ticodendron* do not look like those of *Alnus*—they may assume the fruits came from some other source and not pursue the matter. How many would waste their time to collect a difficult specimen of *Alnus* in primary forest when it could so easily be found along the road? Likewise, even if they do collect it with fruits or flowers attached, they are unlikely to describe it right away if they don't know in which family to place it. The tree looks so familiar and is so common, surely it has already been described! This concept is suggested by field notes on the Lankester specimen: "Woodland tree . . . having a distinctly European appearance."

According to label information, the first botanist to collect *Ticodendron* (see below) thought it might be a genus of Polygonaceae close to *Coccoloba*. A more recent sterile collection, the only one from Nicaragua, was also first identified tentatively as a species of *Ruprechtia* (Polygonaceae). This family is implicated by a conspicuous amlexicaule scar

left on the twigs of *Ticodendron* by the large, paired stipules. Thus, the belated discovery of *Ticodendron* by botanists is curious and yet perhaps explainable by the fact that although it looks very much like something well known, e.g., Polygonaceae, oak or alder, it really is something different.

The earliest known collection of *Ticodendron*, recognized at US by R. Foster, was made in Costa Rica by Carlos Wercklé (probably between 1900 and 1910). Eight other collections (all from Costa Rica, except as indicated) prior to the 1980s have been found: C. H. Lankester (1925), Austin Smith (1938), Steyermark (1942, Guatemala), W. H. Hatheway (1965, 1966), Luis Poveda (1974), and John Pipoly (1979, Nicaragua).

For nearly a decade before specimens from Costa Rica and Panama (1986) began to arrive and arouse interest at the Missouri Botanical Garden, botanists at the Herbario Nacional de Costa Rica had regarded the plant as an unknown of considerable interest, possibly related to Hamamelidales. However, few, if any, others were aware of the existence and significance of this taxon. By then, fruits and male flowers were known; the species was assumed to be dioecious, but female flowers were still needed. When the existence of a fairly common and conspicuous Costa Rican tree that defied identification by the usual route became more widely known, a three-year-long stream of correspondence ensued. The goal was to motivate collectors in Costa Rica and Panama and specialists around the world, from paleobotanists to phytochemists, to gather and analyze the appropriate material in order to place this new tree among its proper relatives.

Distribution and Habitat

The single species of Ticodendraceae is known from southern Mexico to central Panama at elevations from 500 to 2,400 m. A number of collections, most notably those from Mexico, have come to light since the genus was described (Gómez-Laurito & Gómez P., 1989). Below, all known collections are cited. We now have seen specimens from Mexico, Guatemala, Nicaragua, Costa Rica, and Panama, and are confident that other specimens or the plant itself will turn up from the remaining countries of Mesoamerica, where the appropriate habitat occurs.

Specimens examined. MEXICO. OAXACA: Municipio de San Miguel Chimalapa, Cerro Salomón, 1,850 m, 21 Aug. 1986 (fr), *Wendt et al. 5380* (MO); Municipio de Santiago Comaltepec, La Esperanza, 1,600 m, 30 Sep. 1987 (fl & fr), *Luna 49* (MO); Municipio Tontontepec, 2 km SW de Tontontepec, 1,900 m, 17 June 1986 (fr), *Torres & Téllez 8620*. GUATEMALA. HUEHUETENANGO: Cerro Cananá, 2,500–2,800 m, 18 July 1942 (st), *Steyermark 49111* (F). NICARAGUA. ZELAYA: Cerro La Pimienta numbers 1 and 2, 900–1,600 m, 17 Apr. 1979 (st), *Pipoly 5233* (MO). COSTA RICA. ALAJUELA: Cachí, 1,200 m, 27 Sep. 1925 (st), *Lankester s.n.* (US); Reserva Biológica Monteverde, valle del Río Peñas Blancas, 800 m, 30 Mar. 1989 (fl), *Bello 773, 774* (MO); 1 Mar. 1990 (immature fr), *Bello 1971* (MO); 850 m, 28 Mar. 1987 (fl), *Haber & Bello 6840, 6841, 6842* (MO); 29 Mar. 1987 (fl), *6851, 6852* (MO); 900 m, 30 Mar. 1987 (fl & fr), *6868* (MO); 9 Mar. 1987 (bud), *6909* (MO); 800 m, 24 Mar. 1987 (fl), *Haber & Cruz 7071, 7072* (MO); 850 m, 5 Apr. 1987 (fl & fr), *7286, 7604* (MO); 750 m, 12 June 1986 (st), *Hammel et al. 15385* (MO), (fr) *15396* (MO); Reserva Forestal Arenal, Bosque Eterno de los Niños, 1,100 m, 6 Mar. 1990 (fr), *Bello 2154* (MO); Río Aguas Gatas, 1,000 m, 29 Jan. 1990 (fl), *Bello 1877* (MO); Río Caño Negro, 1,200 m, 17 Feb. 1990 (fl), *Bello 1885* (MO); 800 m, 19 Feb. 1990 (fl), *Bello 1911* (MO); Reserva Forestal de San Ramón, 900 m, 26 Feb. 1988 (sapling), *Burger et al. 12452* (CR); 900–1,200 m, 13 Mar. 1987 (st), *Gómez-L. 11403* (CR); 30 Mar. 1987 (fl), *Herrera et al. 515, 516, 517* (MO); Upala, Bijagua, 1,000 m, 9 July 1988 (fr), *Herrera et al. 2032* (MO); Zarcero, La Brisa, 1,800 m, 19 July 1938 (fr), *Austin Smith H970* (F); Zarcero, Volcán Viejo, 1,800 m, 11 Feb. 1986 (fr), *Gómez-L. & Carvajal 11100* (CR). CARTAGO: Reserva Forestal Tapantí, 1,500–2,000 m, 8 July 1986 (st), *I. Chacón 1985* (CR). GUANACASTE: Tilarán, Río Chiquito, 1,100 m, 7 June 1987 (fr), *Haber & Bello 7442* (MO). HEREDIA: Cerro Chompipe, 1,800 m, 17 June 1990 (st), *Hammel et al. 17815* (CR); Sacramento, Montaña La Isla, 2,300–2,500 m, 13 Jan. 1987 (fr), *Gómez-L. 11306, 11307* (CR); 3 Apr. 1987 (fl), *Gómez-L. et al. 11472, 11473* (CR); 17 July 1990 (fr), *Hammel & Rivera 17834* (CR); Volcán Barva, above San José de la Montaña, 1,950 m, 19 Sep. 1965 (fr), *Hatheway 1681* (US); 1 May 1966 (st), *Hatheway 1712* (US). LIMÓN: Cantón de Talamanca, Bratsi, 700 m, 15 July 1989 (st), *Herrera 3339* (CR); Cantón de Guápiles, Río Blanco, 700 m, 24 Feb. 1990 (st), *Herrera & Schik 3791* (CR); Río Blanquito, 1,100 m, 26 Feb. 1990 (fr), *Herrera 3846* (CR); Parque Internacional La Amistad, 650 m, 17 July 1989 (st), *A. Chacón 190* (CR); Reserva Biológica Hitoy-Cerere, 1,024 m, 3 Sep. 1989 (fr), *Hammel et al. 17685* (CR). PUNTARENAS: Cantón de Golfito, Quebrada Vaquedano, 500 m, 23 July 1990 (st), *Herrera 4020*; Monteverde, Quebrada Máquina, 1,400 m, 12 Nov. 1988 (fr), *Bello 447* (MO); 17 Mar. 1990 (immature fr), *Haber 9809* (MO); 14 July 1990 (fr), *Gentry et al. 71474* (MO); Parque Nacional Corcorado, Cerro Brujo, 617 m, 19 July 1990 (st), *Herrera et al. 3969*; Reserva Biológica Monteverde, road to TV tower, 1,600 m, 21 July 1985 (fr), *Haber & Bello 2058* (MO). SAN JOSÉ: Bajo La Hondura, 1,300 m, 21 May 1974 (st), *Poveda 864* (CR); San Cristóbal, 1,650 m, 1900–1910? (fr), *Wercklé s.n.* (US). PANAMA. BOCAS DEL TORO: Fortuna Dam area, 1,250 m, 11 Feb. 1986 (sterile with old fallen fruits), *McPherson & Hammel 8401* (MO). CHIRIQUÍ: Fortuna Dam area, 1,100–1,300 m, 7 Sep. 1987 (st), *McPherson 11659* (MO); 26 Apr. 1988 (fl), *McPherson 12493* (MO); N slope of Volcán Barú, 1,750–1,900 m, 13 Jan. 1989 (st), *McPherson 13525* (MO). COCLÉ: N of El Copé, 750 m, 22 June 1988 (st), *McPherson 12615* (MO).

Ticodendron grows in mid-elevation cloud forests on both sides of the continental divide throughout Mesoamerica. It is most often found in very diverse, evergreen forests wetter and somewhat lower (2,400 m at most) than those dominated by oak, and is typically found on deep, humic soils. At its lowest it descends to 500 m in the Osa peninsula of Costa Rica. Otherwise, in the southern part of its range, where the isthmus is divided sharply by the central mountain chain into wet (Atlantic) and dry (Pacific) sides, the species is more common and descends lower (650 m) on the Atlantic slopes. However, near San José, Costa Rica, numerous populations are known from the very wet southern (Pacific) slopes of the Cordillera Central. In this part of its range *Ticodendron* flowers from January through April, and the fruits mature several months later. Germination has not been observed, but from the numerous young saplings observed we surmise that germination is hypogeal.

Relationships

Even with detailed analyses, which follow, Ticodendraceae finds its position in the Hamamelidae sensu Cronquist (but see Hickey & Taylor, 1991) and Fagales almost by default. Outside Hamamelidae, Euphorbiaceae were considered (because of some similarity to *Picodendron*) but rejected because *Ticodendron* lacks their characteristic obturators (Tobe, 1991). The very reduced unisexual flowers lead by overall similarity to the "higher" Hamamelidae, where many of the old Amentiferae lie. Pollen data also lead there but by way of an array of features unique among dicots (Feuer, 1991; Zavada & Dilcher, 1986).

In the end, Ticodendraceae has been described as a distinct family because it has been shown neither to share any rigorously supported synapomorphy or set of synapomorphies with any taxon already described nor does it fit comfortably in overall similarity within any described family. By a process of elimination, its ordinal placement seemed most likely among Juglandales, Myricales, or Fagales. Urticales were rejected early because *Ticodendron* lacks the foliar trichomes characteristic of that order (Tobe, pers. comm.). *Ticodendron* also does not coincide with Urticales in pistillate flower (Tobe, 1991) and sieve-element characters (Behnke, 1991). *Ticodendron* is eliminated from Juglandales and Myricales because of floral and trichome considerations. Taken together, the details of wood and bark anatomy (Carlquist, 1991), leaf anatomy (Hickey & Taylor, 1991), sieve-element characters (Behnke, 1991), and floral anatomy (Tobe, 1991) suggest that *Ticodendron* cannot be placed exactly within any of the compared families, but that it does not conflict seriously with placement in Fagales. Hickey & Taylor (1991) place *Ticodendron* closest to a fossil, the fagalean genus *Fagopsis*.

Although the pollen data show the highest similarity with Myricaceae (Feuer, 1991), other characters argue strongly against placing *Ticodendron* nearer to Myricales than Fagales. Even the pollen data show considerable similarity with the coryloid Betulaceae (Corylaceae sensu Carlquist). This agrees with the data from bark and wood anatomy (Carlquist, 1991) and sieve-element characters (Behnke, 1991), as well as the observation that the nutlets of *Carpinus* are remarkably similar in shape and sculpturing to (though much smaller than) the endocarp of *Ticodendron*. Although the floral anatomy of *Ticodendron* has a superficial resemblance to *Nothofagus* (Tobe, 1991)—which itself comprises a distinct family, sister to Betulaceae rather than to Fagaceae (cf. Jones, 1986; Nixon, 1989)—among Betulaceae, *Ticodendron* perianth characteristics are more like those of the coryloid genera (Tobe, 1991) (see Table 1).

In Cronquist's (1981) Hamamelidae, *Ticodendron* would find a home in Fagales simply by modifying the key to orders to include plants with hemitropous ovules. On the basis of floral anatomy (Tobe, 1991) and wood and bark anatomy (Carlquist, 1991), Ticodendraceae would be more primitive within Fagales than other families. With our present knowledge, the best estimate of relationships of *Ticodendron* is represented by placing it in its own family within the order Fagales, where it is distinctive for its drupaceous fruits, four-loculed ovary, and hemitropous ovules.

Biogeography

Ticodendraceae is endemic to Mesoamerica, and by virtue of its alliance to the higher Hamamelidae is probably a remnant of the Tertiary Laurasian flora. As such, its discovery and distribution are significant at a level with the trigonobalanoid Fagaceae of Colombia, *Alfaroa* and *Oreomunnea* (Juglandaceae), *Molinadendron* and *Matudaea* (Hamamelidaceae), and *Nyssa talamancana* Hammel & Zamora (Cornaceae) (see Hammel & Zamora, 1990; Nixon & Crepet, 1989; van der Hammen & Cleef, 1983). The fossil histories of these or related taxa tell us that they are remnants of a once widespread northern forest. Indeed, according to leaf characteristics (Hickey & Taylor, 1991) *Ticodendron* appears to be most closely related to a fossil from Oligocene deposits in Colorado. The rather obvious extrapolation is that fossils of *Ti-*

TABLE 1. Characteristics of *Ticodendron* and some of the taxa with which it has been compared. Data are mostly from papers in this compendium and Cronquist (1981).

	TICO[a]	OSTR	BETU	MYRI	ULMA	HAMA	NOTH	JUGL	PICR	CECR	CASU
PERIANTH											
Male	absent	=[b]	x	=	x	x	x	x	=	x	=
Female	present	=	x	x	=	=	=	=	x	=	x
POLLEN	triporate	=	=	=	x	x	x	=	x	?	=
Endexine	absent	=	x	=	x	±	x	x	?	?	x
STYLES	2	=	=	=	=	=	±	=	=	1	=
CARPELS	2	=	=	=	=	=	±	=	=	1	=
LOCULES	4	2	2	1	x	2	2 or 3	1	2	1	2
OVULE	1/locule	2	=	=	=	=	2	=	2	=	2
	pendulous	=	=	erect	=	=	=	erect	=[c]	?	erect
Placentation	axile	=	=	basal	apic	=	=	basal	=	basal	?
	hemitropous	ana	ana	ortho	ana	ana	ana	ortho	?	ortho	=?
	unitegmic	=	=	=	bi	bi	=	=	bi	bi	bi
FRUIT	drupe	nut	nut	=	=	caps	nut	=	=	±	nut
	no cupule	=	=	=?	=	=	x	=	=	=	x?
SEEDS	1	=	=	=	=	x	=	=	=	=	=
LEAVES	simple	=	=	=	=	=	=	x	x	=	?
STIPULES	present	=	=	x	=	=	=	x	=	=	x
SHARED											
(= or ±)	17	13	11	11	10	10	9	9	9	7	6

[a] Expansion of abbreviations of taxa: *Ticodendron*, *Ostryopsis*, *Betula*, *Myrica*, Ulmaceae, Hamamelidaceae, *Nothofagus*, *Juglans*, *Picrodendron*, Cecropiaceae, Casuarinaceae.

[b] Symbols are compared to *Ticodendron*: = same as, x different, ± variable but including, ? unknown or uncertain; where convenient the character state itself is presented.

[c] Ovules pendulous from an obturator.

codendron and its associated Laurasian taxa must exist and ought to be sought in North America, Europe, and Asia.

Both the high mountains and lowlands of southern Central America have floras dominated by relatively recently (ca. Pliocene) arrived taxa; the rising mountains were invaded by northern species and the lowlands by South American species across the isthmus (Gentry, 1982b; Grayum & Churchill, 1987; Hammel, 1986; Rich & Rich, 1983; Standley, 1937). However, *Ticodendron* and all of the other above-mentioned Laurasian taxa, endemic to the region between southern Mexico and northern Columbia, are found for the most part in wet to moist mid-elevation forests. These areas, more than anywhere else in the tropics, are characterized by the kind of mild, humid and aseasonal climate that was prevalent across the Northern Hemisphere in Paleogene (65–25 mya) times. Further exploration and careful phytogeographical analysis in the areas where *Ticodendron* grows, especially along the isolated, wet Caribbean slopes is likely to reveal additional archaic forms that may, in some cases, give us direct, living insight into the kinds of species widespread in the northern forests tens of millions of years earlier.

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WOOD AND BARK ANATOMY OF *TICODENDRON*: COMMENTS ON RELATIONSHIPS

Sherwin Carlquist[1]

ABSTRACT

The single known species of *Ticodendron* has notably primitive wood (scalariform perforation plates with numerous bars; primary wall remnants in perforations; scalariform lateral wall pitting in vessels; imperforate tracheary elements all tracheids; axial parenchyma diffuse; rays Heterogeneous Type I). Although wood of Betulaceae and Corylaceae (Betulaceae subfamily Coryleae of most authors) is more specialized, primarily in tracheary element morphology and ray histology, wood features in these families are consonant with relationship to *Ticodendron*. Presence of crystals in rays is alike in *Ticodendron*, Corylaceae, and Fagaceae. Bark anatomy features are shared by the fagalean families: fusiform-shaped nests of sclereids containing large rhomboidal crystals; druses in cortex, phloem parenchyma, and ray parenchyma; and subdivision of ray cells that contain druses. Placement of *Ticodendron* in Fagales as a separate family, more primitive than others in the order, is indicated by the data reviewed.

Wood anatomy is of interest in phylogenetic studies because it contains characters that suggest relationship, as well as characters that are sensitive indicators of ecology and of degree of primitiveness and specialization. Bark anatomy, if not as rich in characters, does contain certain character assemblages indicative of relationship. The discovery of the distinctive tree *Ticodendron* (Gómez-Laurito & Gómez P., 1989) provides an opportunity for the use of wood and bark anatomy in order to determine the relationships of this interesting genus.

The samples of *Ticodendron*, provided me by Peter H. Raven and Barry Hammel of the Missouri Botanical Garden, proved excellent material for analysis of anatomical features. Liquid-preserved stems 37 mm diam. with thin bark were collected by Gordon McPherson (*11659*, MO) at Fortuna Dam, Chiriquí, Panama. A dried section of a large log (about 40 cm diam.) with bark 6 mm thick was collected by William A. Haber (*7071*, MO) at Peñas Blancas, east of Monte Verde, Costa Rica. Viewed together, these samples permit study of a broad range of histologic and ontogenetic aspects of wood and bark.

Comparison of wood and bark anatomy of *Ticodendron* with that of other dicotyledons is the main focus of this study because of the distinctive features and apparent isolation of the genus. For this purpose, the wood slide collection at the Rancho Santa Ana Botanic Garden proved unusually valuable because of its size and because some of the wood sections in this collection have bark attached to them. The data below show that bark seems unusually decisive in determination of relationships of *Ticodendron*.

Regardless of systematic position, *Ticodendron* possesses a constellation of characters that must be judged unusually primitive for a vessel-bearing dicotyledon. These wood features offer an unusual dimension, because one might not have guessed that the moderately specialized floral features of the genus are coupled with such primitive wood. Wood of this type is related to occupancy of mesic sites (Carlquist, 1975), and thus wood of *Ticodendron* is of interest with relationship to ecology as well.

MATERIALS AND METHODS

A wood segment from near the cambium and a bark portion were taken from the large dried trunk section *Haber 7071*. These were boiled in water and stored in 50% aqueous ethyl alcohol. Similar segments of *McPherson 11659*, a liquid-preserved collection, were transferred to 50% aqueous ethyl alcohol. Wood and bark of both collections were sectioned on a sliding microtome without softening agents. Some sections of *McPherson 11659* were dried between glass slides and examined with a scanning electron microscope. Sections for light microscope study were stained in safranin and lightly counterstained with fast green to improve con-

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trast of pit details. Macerations were prepared with Jeffrey's fluid and stained with safranin.

Mean number of vessels per group is calculated on the basis that a solitary vessel is rated 1, a pair of vessels in contact is rated 2, and so forth, and 25 such figures are averaged. Vessel diameter is based on lumen diameter at widest point. Means for quantitative features are based on 25 measurements except for vessel wall thickness, tracheid diameter, and tracheid wall thickness; for these features, a few typical conditions were selected and averaged.

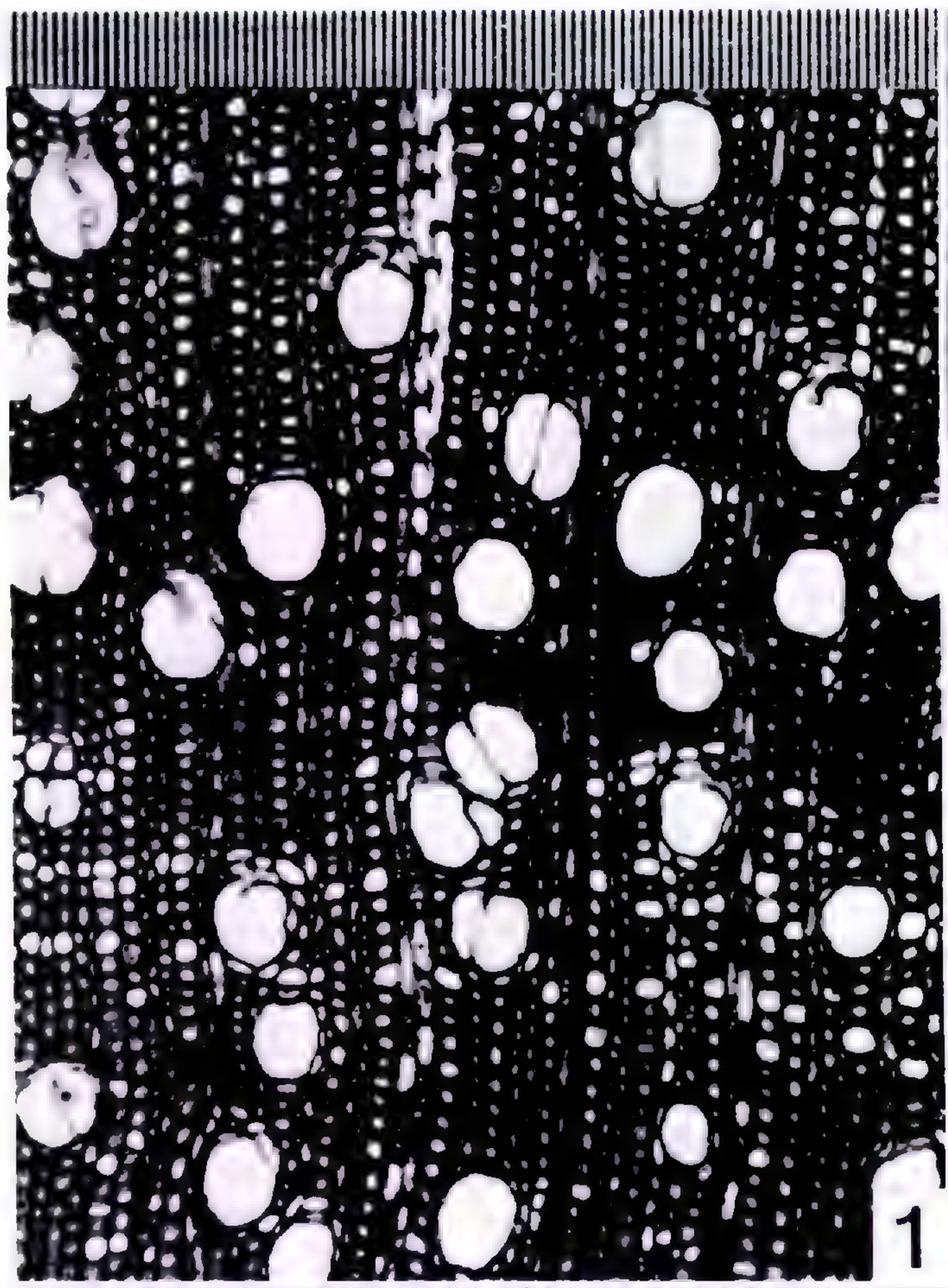
Anatomical Descriptions

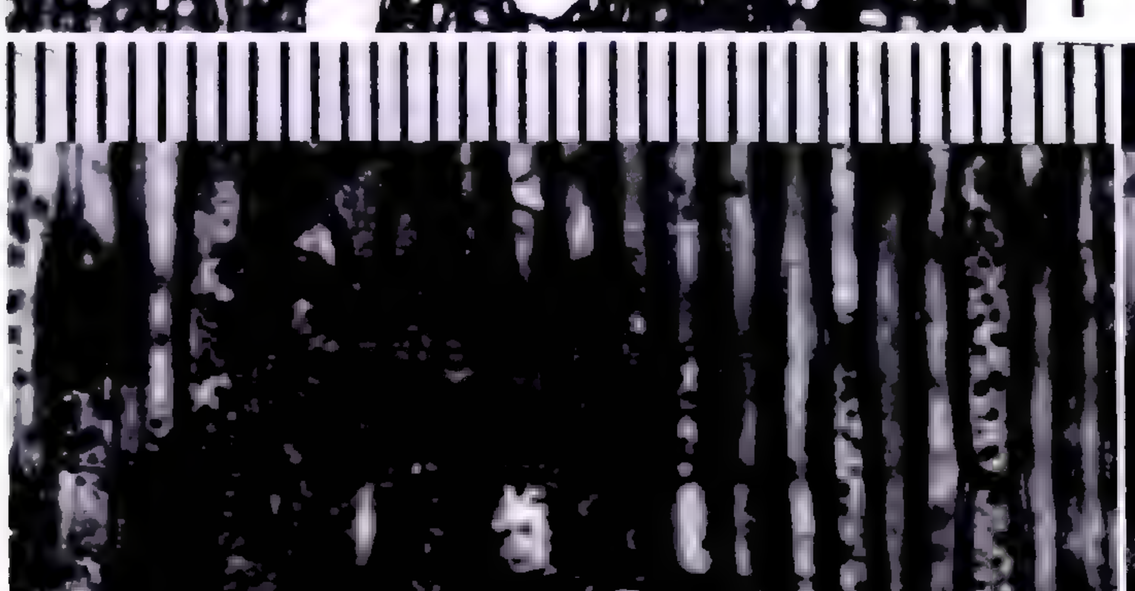
wood

A full description is given here for the sample *McPherson 11659*. Data are then given for *Haber 7071*, but the latter description is limited to features in which this wood sample differs from *McPherson 11659*.

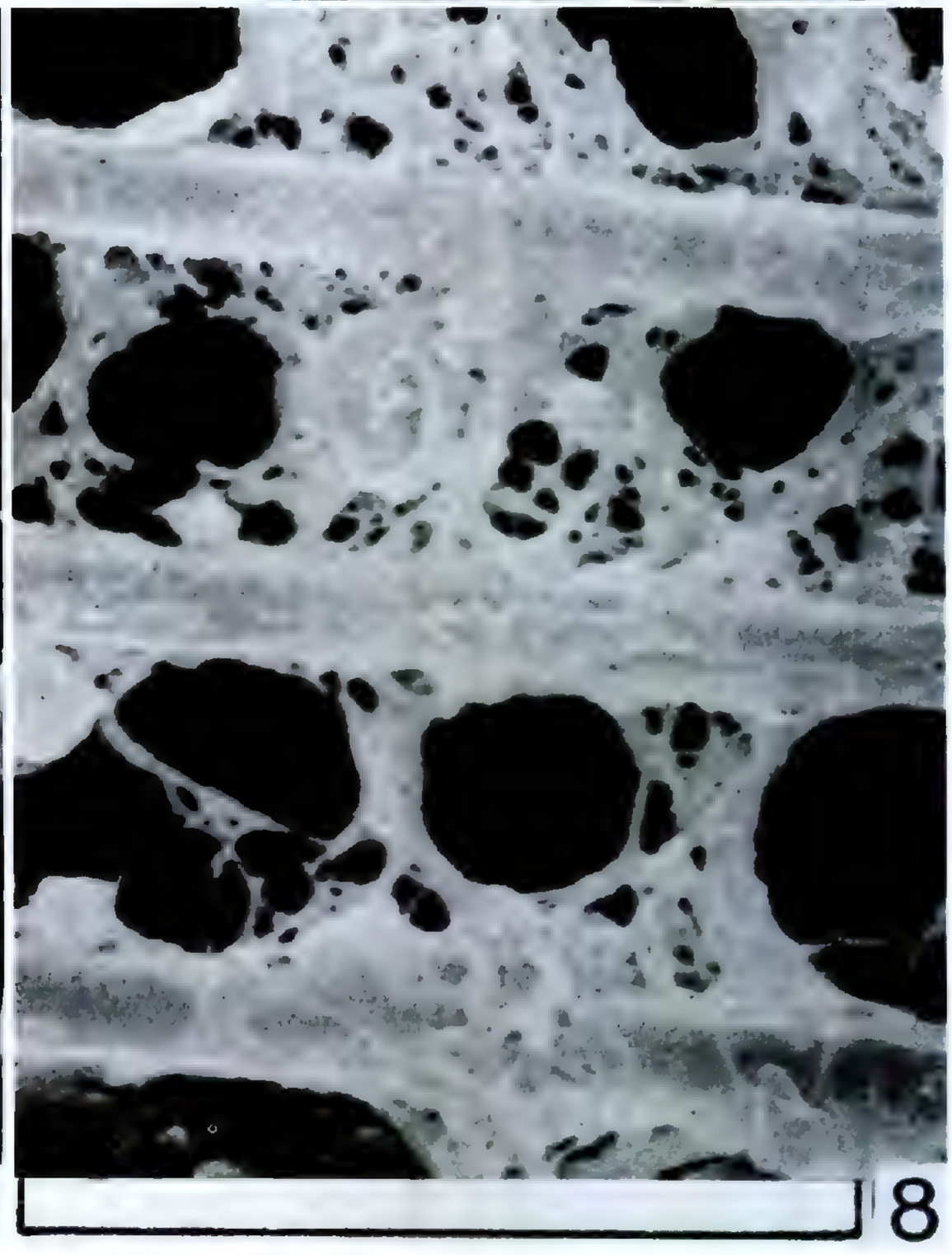
Ticodendron incognitum Gómez-Laurito & Gómez P., *McPherson 11659* (Figs. 1–15). Growth rings essentially absent; a small fluctuation in vessel diameter observable (narrower vessels one-third of the way from bottom of photo, Fig. 1). Vessels solitary, rarely in pairs (Fig. 1). Mean number of vessels per group, 1.04. Mean vessel diameter, 73 μm. Mean number of vessels per mm², 23. Mean vessel element length, 1,725 μm. Mean vessel wall thickness, 2.6 μm. Perforation plates scalariform (Figs. 6, 7), all bars bordered, borders wider at ends of perforations (Fig. 7). Mean number of bars per perforation, 62. Perforation plates frequently with meshlike pattern in this sample (Figs. 9–11). Primary wall remnants in perforation plate extensive (Figs. 6, 10, 11) to moderate (Figs. 7, 8), mostly the latter, but with some vestiges of pit membranes present in all perforation plates. Moderate remnants take the form of webs and strands (Figs. 7, 8), or have a clotted appearance (Fig. 11), the latter possibly the result of inhibition of enzymatic pit membrane dissolution by deposition of some secondary plant products. Primary wall remnants in perforations may show various sizes of micropores (Fig. 8). Lateral wall pitting of vessels scalariform, less commonly transitional or opposite, on vessel–axial parenchyma (Fig. 13) and vessel–ray contacts. Vessel–tracheid contacts bear circular to oval pits alternate in arrangement but often rather sparse (Fig. 12). Vessels rounded in transectional outline (Fig. 1). Imperforate tracheary elements are all tracheids with fully bordered pits, pit cavities about 4 μm diam. (Fig. 5). Mean tracheid length, 2,473 μm. Mean tracheid diameter at widest point, 29 μm. Mean tracheid wall thickness, 6 μm. Pits are somewhat more abundant on tangential walls of tracheids than on radial walls, as determined from study of transections. Axial parenchyma moderately abundant and chiefly diffuse, with tendencies toward diffuse-in-aggregates and abaxial occurrence (Fig. 1). Axial parenchyma strands often about 14 cells long, the mean length of each component cell about 150 μm. Rays both multiseriate and uniseriate, about equal in frequency (Fig. 2). Mean height of multiseriate rays, 1,193 μm. Mean height of uniseriate rays, 594 μm. Mean width of multiseriate rays at widest point, 3.2 cells. Multiseriate rays mostly with a uniseriate wing at one or both tips. Uniseriate rays and uniseriate wings of multiseriate rays composed of upright cells. Upright cells also present adjacent to wings of multiseriate rays and occasional as sheath cells in multiseriate rays (Fig. 2). Procumbent cells present in multiseriate portions of multiseriate rays, not much longer horizontally than vertically (Fig. 3). Rhomboidal crystals present singly in a scattering of ray cells (Fig. 4), the crystals more abundant in the transition from one year's wood to the next. Starch grains spherical (Fig. 14) to slightly angular (Fig. 15), abundant in axial parenchyma (Figs. 3, 14) and in ray cells (Figs. 4, 15). Dark-staining "resinlike" compounds present in many (but not all) ray cells (Figs. 2–4). Unidentified smaller spheroidal bodies present in ray cells (Fig. 15).

Ticodendron incognitum, Haber 7071. Mean number of vessels per group, 1.13. Mean vessel diameter, 116 μm. Mean number of vessels per mm², 22. Mean vessel element length, 1,782 μm. Mean vessel wall thickness, 2.6 μm. Perforation plates scalariform (no meshworklike patterns observed). Mean number of bars per perforation plate, 32. Primary wall remnants in perforations (as observed by light microscopy) minimal. Mean tracheid length, 2,537 μm. Mean tracheid diameter at widest point, 31 μm. Mean tracheid wall thickness, 7.2 μm. Axial parenchyma diffuse (sparser than in *McPherson 11659*), with a slight tendency toward diffuse-in-aggregates and abaxial arrangements. Mean height of multiseriate rays, 2,312 μm. Mean height of uniseriate rays, 525 μm. Mean width of multiseriate rays at widest point, 6.0 cells. Uniseriate rays and uniseriate wings of multiseriate rays composed of upright cells. Multiseriate portions of multiseriate rays composed of procumbent cells, with only a few upright sheathing cells present. Procumbent cells radially elongate (radial dimension 1.5–8× the vertical dimension). Crystals

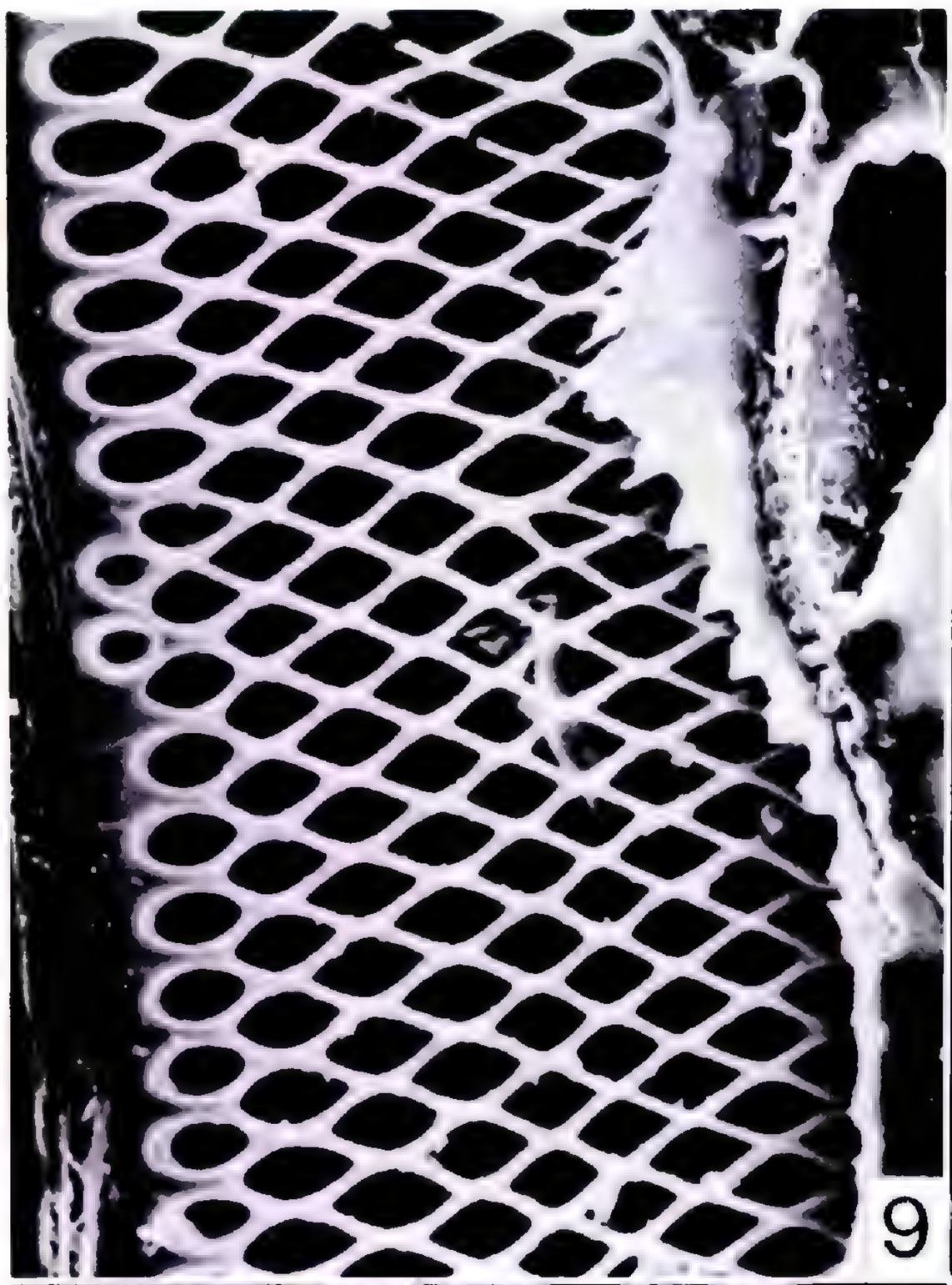


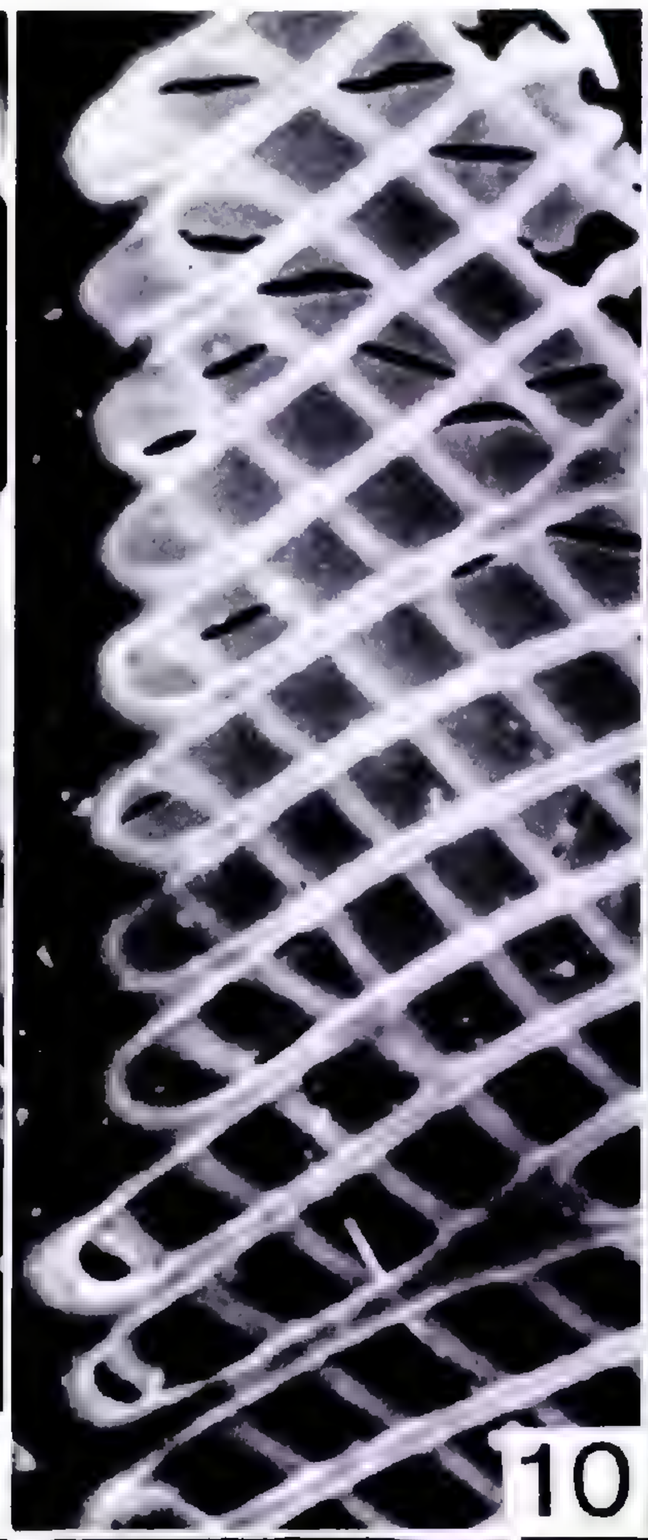


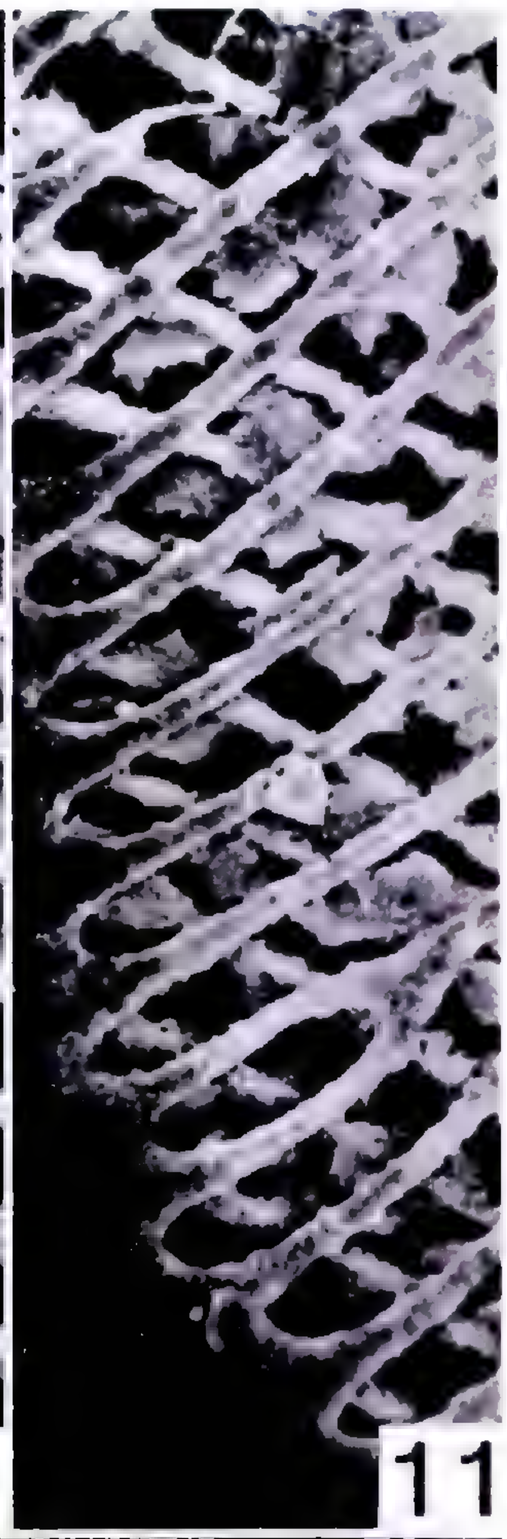
FIGURES 1–4. Wood sections of *Ticodendron incognitum, McPherson 11659*.—1. Transection; vessels are solitary (pair of vessels in contact, center).—2. Tangential section; rays conform to Kribs's Heterogeneous Type I.—3. Radial section; ray in sectional view, showing starch (hila = dark dots) and dark-staining compounds; cell shapes vary between square and upright.—4. Radial section, showing rhomboidal crystal, starch grains, and dark-staining compounds. Figures 1, 2, magnification scale above Figure 1 (divisions = 10 μm). Figure 3, scale above Figure 3 (divisions = 10 μm). Figure 4, scale above Figure 4 (divisions = 10 μm).

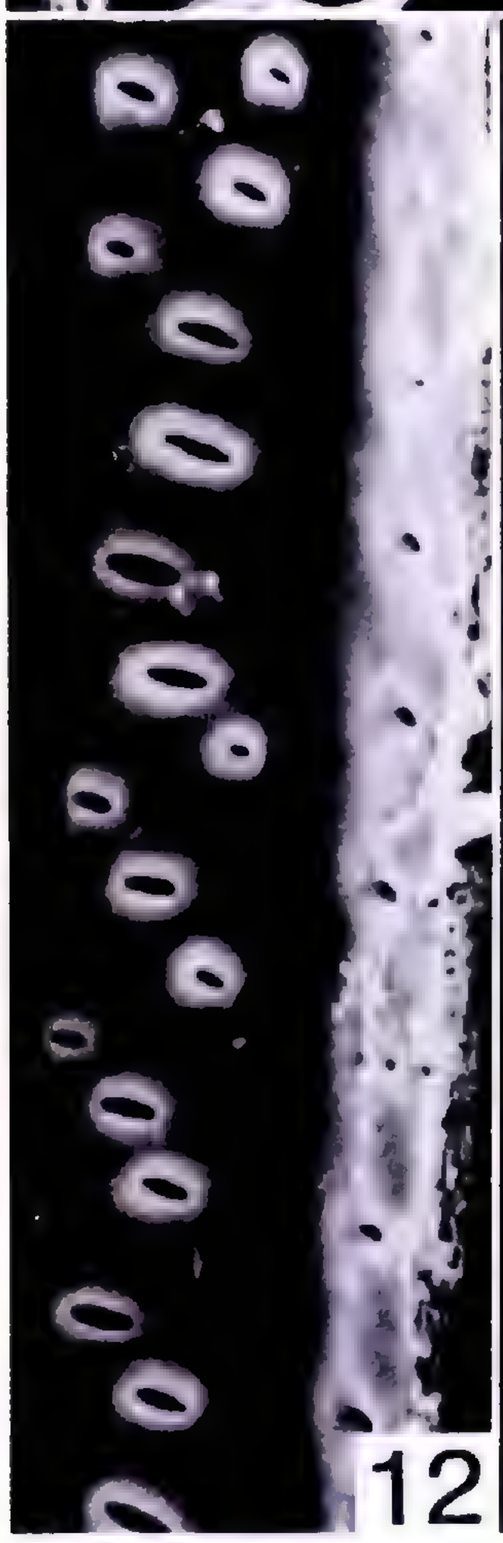


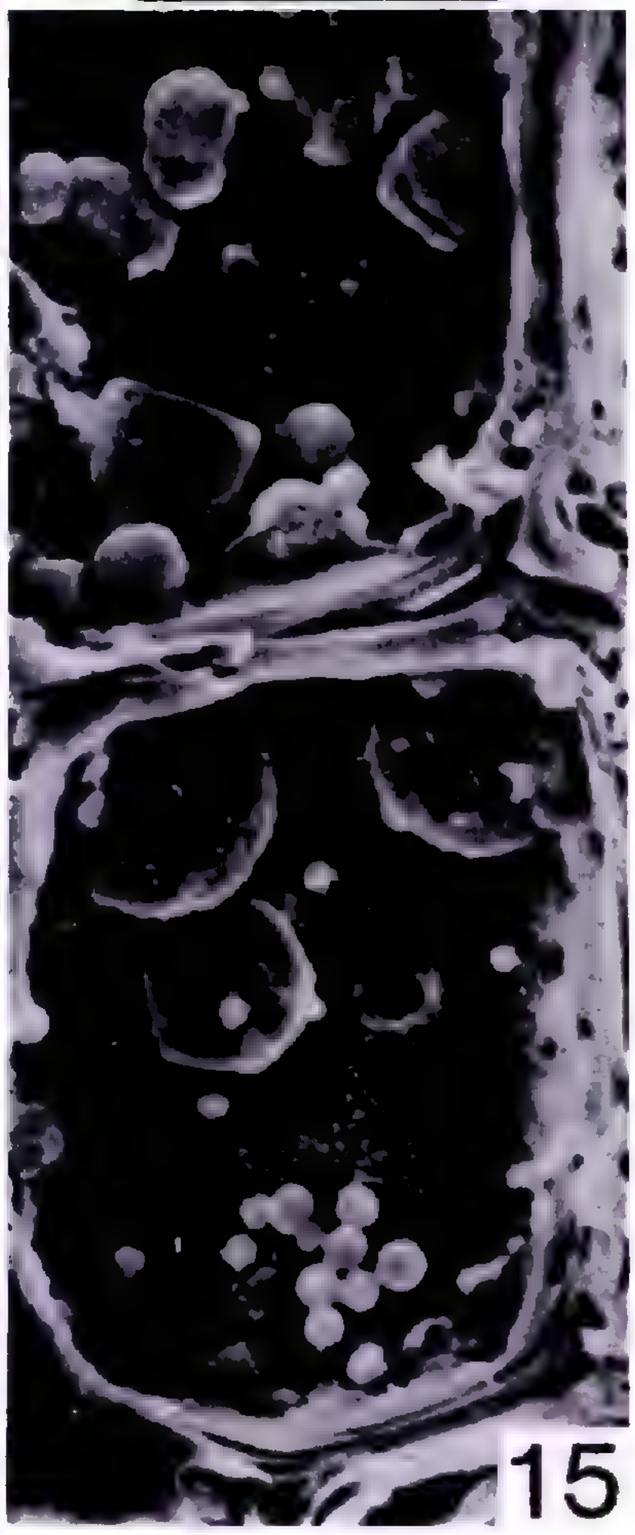
FIGURES 5–8. Wood sections of *Ticodendron incognitum, McPherson 11659.*—5. Radial section, showing pits on tracheid in face view (center) and sectional view (left). 6–8. Perforation plates from radial sections, SEM photographs.—6. Perforation plate bearing large intact portions of pit membranes.—7. Perforation plate bearing threadlike and weblike portions of pit membrane.—8. Perforation plate portion, showing micropores among microfibrillar webs of pit membranes in perforations. Figure 5, magnification scale above Figure 4. Figures 6–8, scale indicating magnification (bracket = 10 μm at bottom of respective figures).











FIGURES 9–15. SEM photographs of wood sections of *Ticodendron incognitum, McPherson 11659*. 9–11. Perforation plates from radial sections, showing meshlike patterns.—9. Perforation plate with minimal remnants of pit membranes.—10. Perforation plate portion with nearly intact pit membranes in perforations.—11. Perforation plate portion with irregularly dislodged pit membrane portions.—12. Vessel—tracheid pitting from radial section (vessel side shown). –13. Vessel—axial parenchyma pitting from radial section (vessel side shown).—14. Starch grains in axial parenchyma cell, from radial section.—15. Starch grains and smaller spheroids in ray cells, from radial section. Figure 9, magnification scale at bottom of Figure 7. Figures 10–15, magnification scale at bottom of Figure 6.

occasional in ray cells (more abundant than in *McPherson 11659*).

The ways in which *Haber 7071* differs from *McPherson 11659* are to be attributed most to different sizes and therefore ages of the samples. Although the wood of *McPherson 11659* does not represent a juvenile pattern, its features can be described as more mature than *Haber 7071* with respect to vessel diameter, multiseriate ray height and width, and degree of radial elongation of procumbent ray cells. The meshlike perforation plate pattern, so abundant in *McPherson 11659*, may be a juvenile feature. This pattern is perhaps less an anomaly than one might think. If a vessel in which bars of a perforation plate follow an oblique or diagonal pattern rather than a strictly horizontal one, a meshlike pattern occurs where the perforation plates (which are combinations of secondary walls of two adjacent cells) occur. The two collections differ slightly in crystal abundance, a feature that sometimes is related to age in dicotyledons.

BARK

The collection *McPherson 11659* (Figs. 16–19) is used as the basis for description; features by which *Haber 7071* differs are given in a later paragraph.

Druses are present in cortical cells (Fig. 17, right), phloem ray cells (center strip two cells wide, Fig. 18), and axial phloem parenchyma cells (Fig. 18, upper left and lower right). Only a fraction of the axial phloem parenchyma cells contain druses. Thus, when axial phloem parenchyma cells develop thick lignified walls (Fig. 17), only a few of these sclereids contain druses. Druses occur in "chambered" fashion in ray cells that are subdivided horizontally, each cell with a single druse.

In older parts of the secondary phloem (Fig. 17), sclereids derived from sclerification of axial phloem parenchyma cells occur in patches. Analysis of longisections shows that these sclereids are not fibers, because they are subdivided into strands as are xylem axial parenchyma; they are also wider than fibers typically are.

Nests of sclereids form in the cortex (Fig. 19), as well as in the old secondary phloem. In the phloem, the sclereid nests evidently are derived from axial phloem parenchyma, but develop into cells much larger and more nearly isodiametric in shape than the sclereid strands mentioned in the above paragraph. In three dimensions, the sclereid nests are often fusiform in shape, the long axis paralleling the stem axis. Many of these sclereids contain one large rhomboidal crystal each (Fig. 19).

The surface of *McPherson 11695* (Fig. 16, top) demonstrates a periderm with about 10 layers of highly compressed phellem cells; this periderm is a dark band in this photograph.

Dark-staining compounds are evident in many cells of the secondary phloem (Figs. 16–19). Cells that contain druses usually do not also contain the dark-staining compounds.

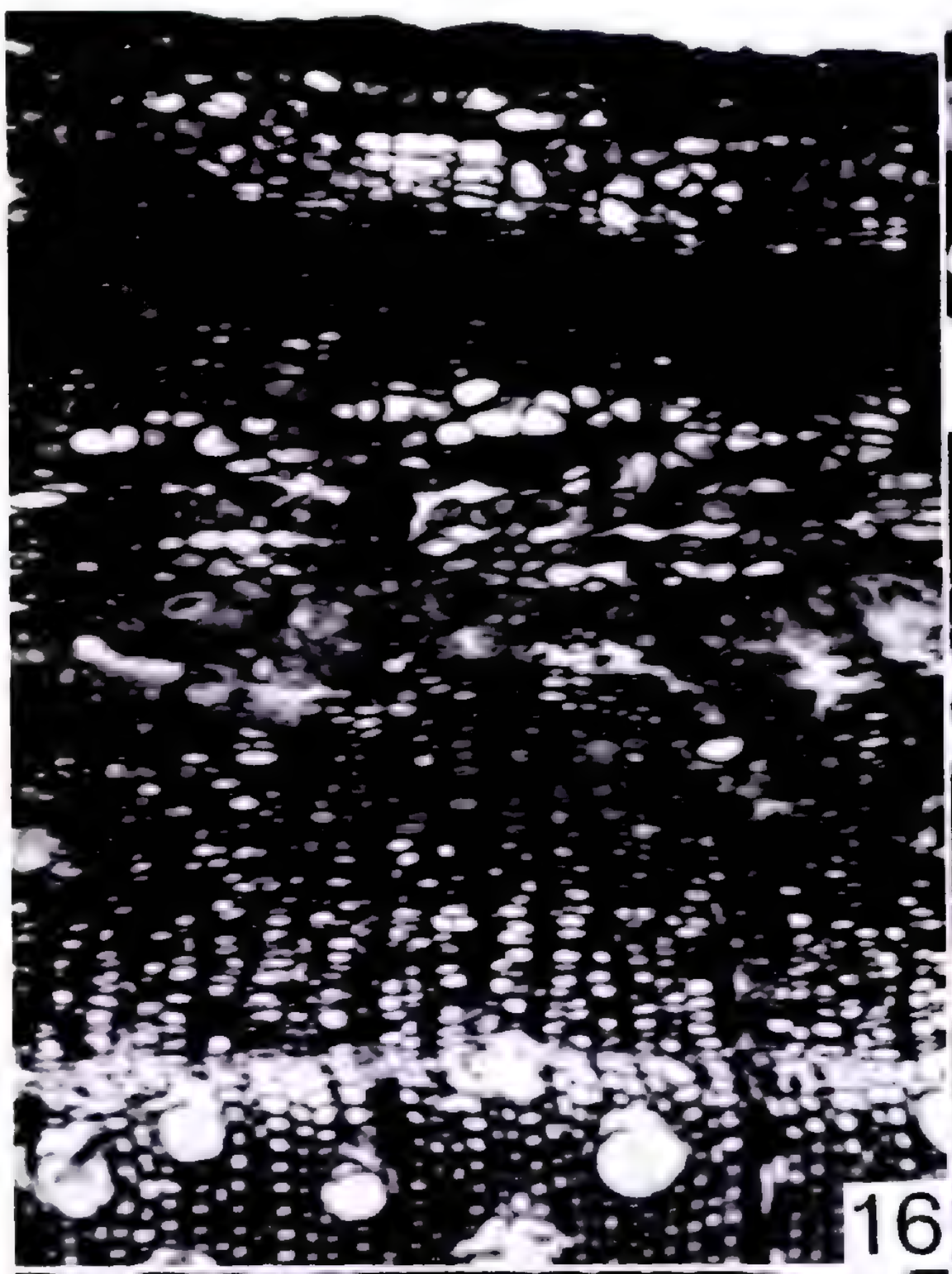
The thick bark of *Haber 7071* reveals several differences. Periderm was not observed in this bark; evidently it had sloughed off and no new periderms originate at levels deep in the bark. *Haber 7071* contains a large number of patches of the sclerified phloem parenchyma strands, but nests of large sclereids, some of which cells contain rhomboidal crystals, are also present. These differences are probably related to age rather than to genetic distinctness.

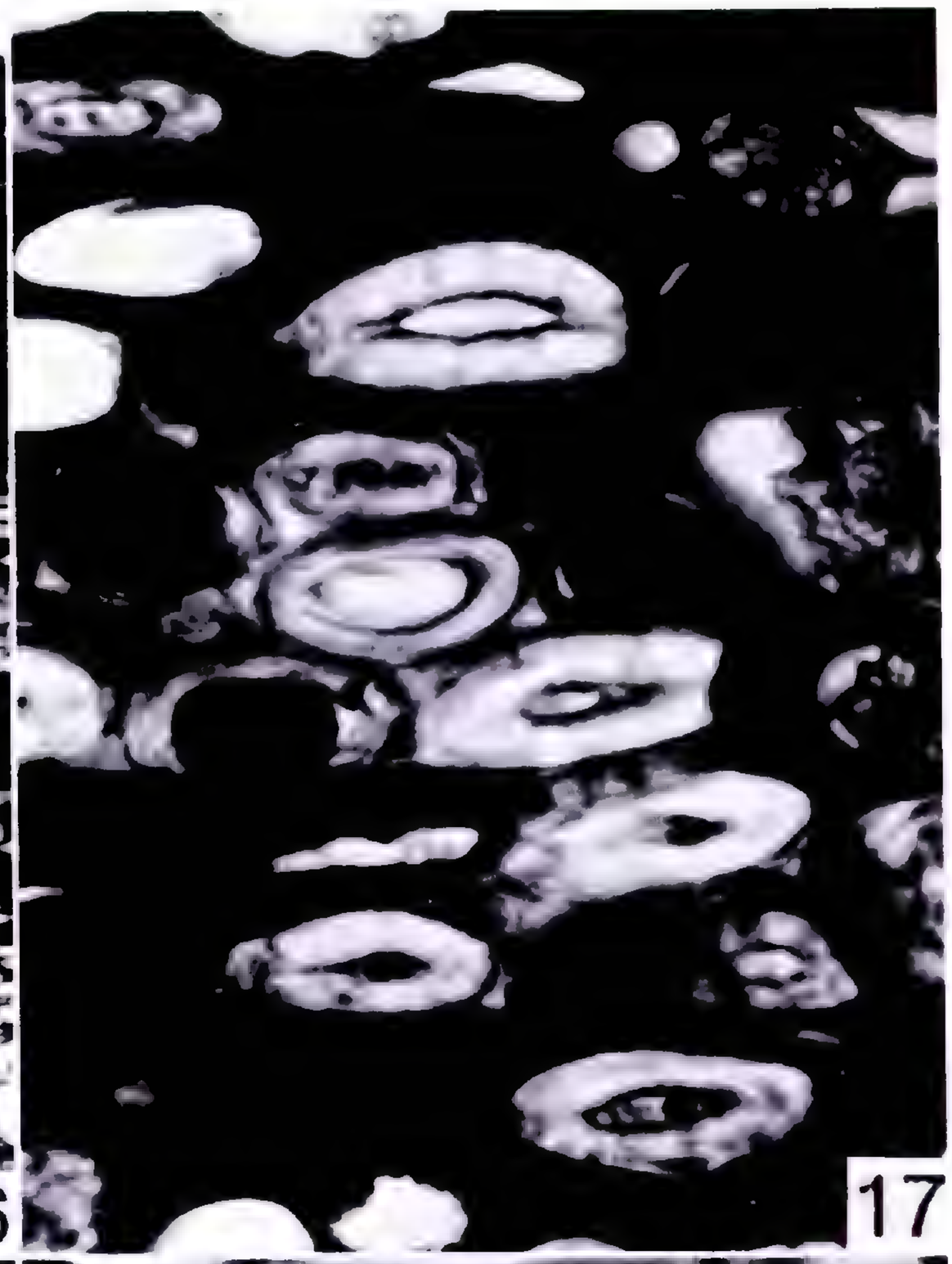
RELATIONSHIPS OF *TICODENDRON*

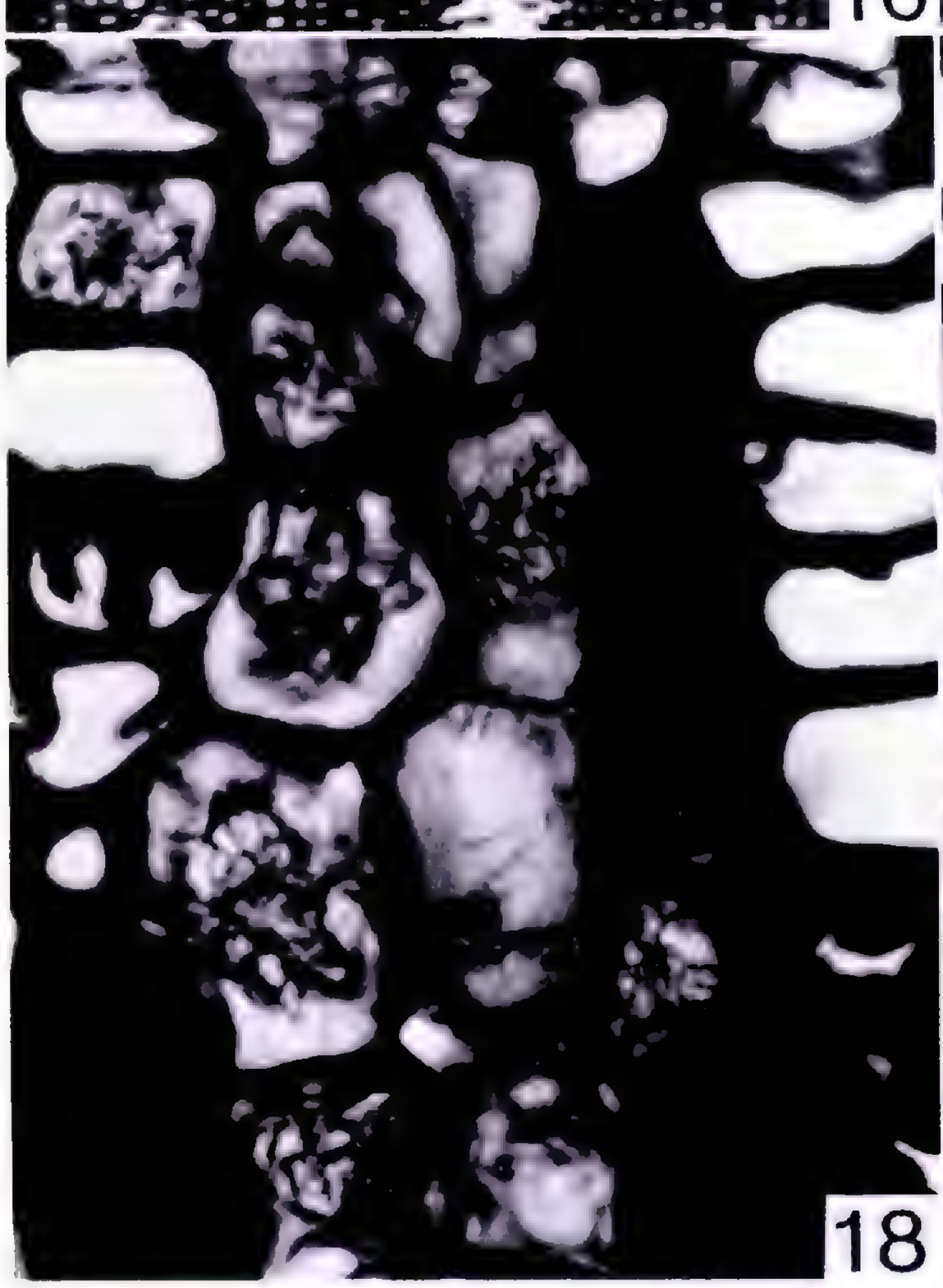
Wood of *Ticodendron* is exceptionally rich in primitive features. This suggests unbroken occupancy by this phylad of mesic areas, according to earlier considerations (Carlquist, 1975). Features of *Ticodendron* wood that are regarded as primitive and the authorities for those interpretations in dicotyledons at large are as follows: long vessel elements (Bailey & Tupper, 1918); perforation plates scalariform with numerous bordered bars (Frost, 1930); perforation plates with remnants of pit membranes (Carlquist, 1988: 56–60); tracheids present as the imperforate tracheary element type (Metcalfe & Chalk, 1950: xlv, "fibers with distinctly bordered pits"); axial parenchyma diffuse (Kribs, 1937); rays Heterogeneous Type I (Kribs, 1935). Primitive wood features are not by themselves evidence of relationship, for they may be retained in many phylads of dicotyledons independently.

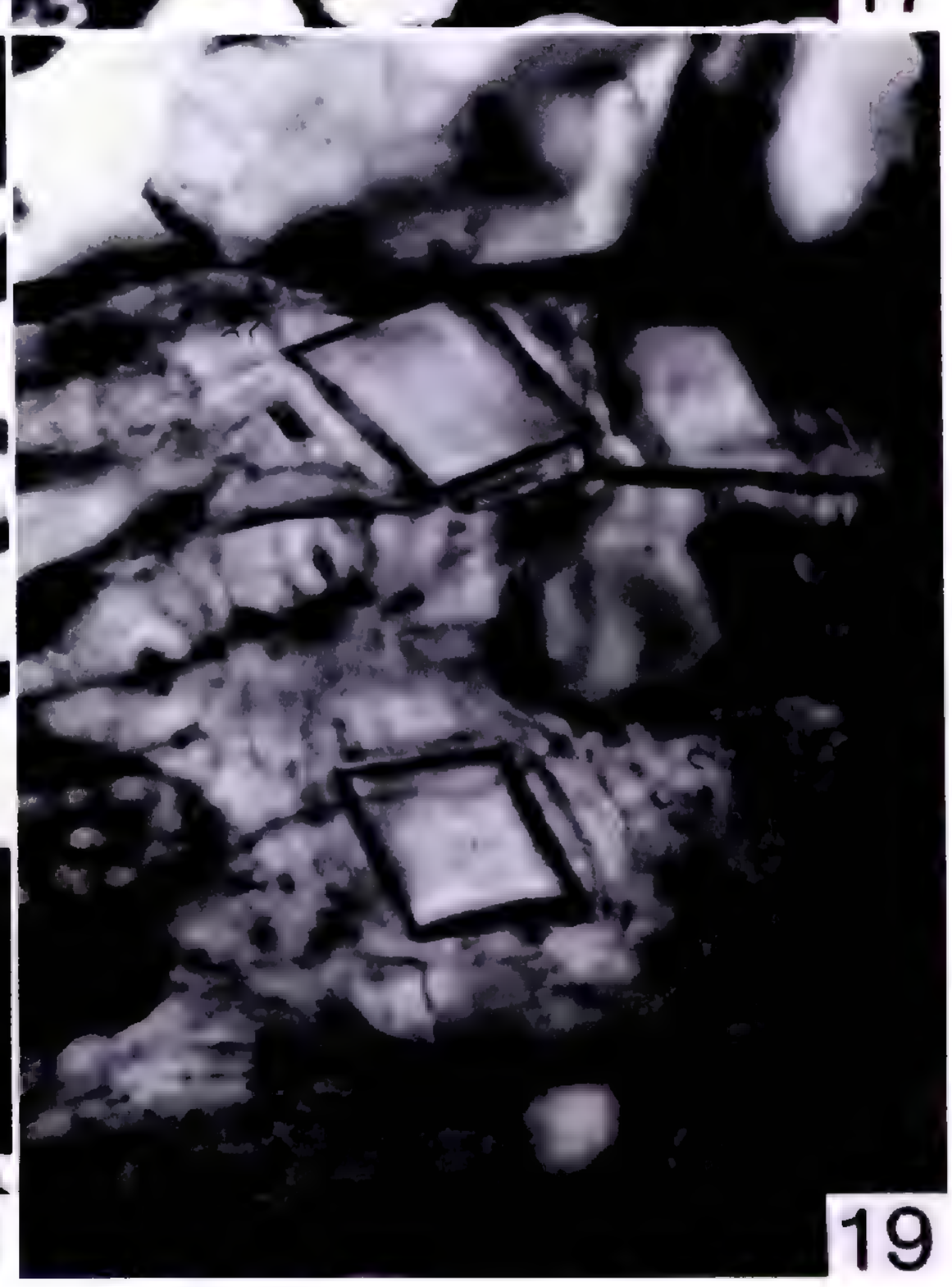
The presence of crystals in rays of *Ticodendron*, a feature that is neither primitive nor specialized, is not evidence of relationships because the number of families that have rhomboidal crystals in rays is quite large (Carlquist, 1988: 225–228). Crystal presence in wood also must be interpreted in a larger context: crystals are more often present in leaves and in primary stems than in wood, suggesting that absence of crystals in wood should be considered significant only if crystals are also absent elsewhere in the plant.

In searching for woods that may resemble that of *Ticodendron*, difference in evolutionary level (especially if moderate) does not rule out relationship provided that there are no features with distinctive systematic distribution that would contra-









FIGURES 16–19. *Ticodendron incognitum, McPherson 11659*, views of bark transections.—16. Transection; small portion of secondary xylem, below, periderm at top (dark); sclereid nests, center (gray).—17. Sclerified axial phloem parenchyma cells.—18. Druses in secondary phloem ray (center strip two cells wide) and in adjacent phloem parenchyma cells (upper left, lower right).—19. Portion of sclereid nest with prominent rhomboidal crystals. Figure 16, magnification scale above Figure 1. Figures 17–19, magnification scale above Figure 4.

dict relationship (e.g., presence of vestured pits, presence of intraxylary phloem). Such features have distinctive systematic distributions but are not found in *Ticodendron*. The wood of Betulaceae differs moderately from that of *Ticodendron* in degree of phyletic advancement (data from Tippo, 1938, and Metcalfe & Chalk, 1950). In Betulaceae, perforation plates are scalariform with numerous bars and axial parenchyma is diffuse as in *Tiocodendron*. Somewhat more specialized in Betulaceae than the corresponding feature in *Ticodendron* is the presence of the fiber-tracheids (rather than tracheids). The rays of Betulaceae (Homogeneous Type I and III) are markedly more specialized than those of *Ticodendron* (Heterogeneous Type I), as is the alternate pitting of vessels (as compared to scalariform to opposite). Rhomboidal crystals are not present in wood of Betulaceae, but they are present in vegetative parts of the plant. Woods of Betulaceae may contain dark-staining deposits like those of *Ticodendron*.

Wood of Corylaceae (Betulaceae subfamily Coryleae of many authors) also shows resemblances to *Ticodendron*, but about the same degree of divergence in level of specialization (data from Tippo, 1938, and Metcalfe & Chalk, 1950). In Corylaceae, perforation plates range from scalariform to simple and lateral wall pitting is alternate; fiber-tracheids are present; axial parenchyma is diffuse; rays are Homogeneous Type II, or have a small degree of heterogeneity (Heterogeneous Type IIB) in *Carpinus* and *Ostrya*. Wood of Corylaceae often contains dark-staining deposits like those of *Ticodendron*.

The occurrence of grouped vessels in Betulaceae and Corylaceae is not a specialized character independent of others. Vessels may be grouped in woody dicotyledons with fiber-tracheids or libriform fibers (degree of grouping depends on ecology), but vessels are solitary or nearly so in woods with tracheids (Carlquist, 1984), as in *Ticodendron*. Rhomboidal crystals, like those of *Ticodendron*, do occur in rays of Corylaceae.

There are no distinctive characters of systematic significance in woods of Betulaceae or Corylaceae that are not also found in *Ticodendron*. Fagaceae has many of the same features as Betulaceae and Corylaceae (e.g., crystals in ray cells), but wood is rather more specialized. Thus, comparisons to *Ticodendron* need not involve Fagaceae.

Bark anatomy, however, more clearly shows relationship between *Ticodendron* and the fagalean families (observations on these families original, based on material in the Rancho Santa Ana Botanic Garden wood slide collection). Fusiform nests of sclereids, cells of which contain large rhomboidal sclereids, are found in bark of *Ticodendron*, *Corylus cornuta* Marsh. (= *C. rostrata* Ait.), *Betula pendula* Roth, and, in Fagaceae, *Lithocarpus densiflora* (H. & A.) Rehder. These highly distinctive sclereid nests alone might be evidence of relationship. In addition, druses in cortex, axial secondary phloem parenchyma, and phloem ray parenchyma characterize *Ticodendron*, *Betula pendula*, and *Corylus cornuta* (druses in cortex but rhomboidal crystals in axial phloem parenchyma occur in *Lithocarpus densiflora*). Subdivided phloem ray cells with a druse in each of the cells occur in *Ticodendron* and *Corylus cornuta*. *Ticodendron* does not have phloem fibers, but it has a possibly allied phenomenon, conversion of strands of axial phloem parenchyma to strands of sclereids. Phloem fibers do occur in *Betula pendula* and *Corylus cornuta*. Phloem fibers are absent in bark of some species of *Betula* and *Alnus*. *Ticodendron* has an external periderm, but evidently does not develop successive deep-seated periderms; deep-seated periderms are likewise absent in *Alnus*, *Betula*, and at least some Fagaceae.

Thus, there are no features in wood that rule out a relationship between *Ticodendron* and the families of Fagales (Betulaceae, Corylaceae, Fagaceae). The similarity in bark between *Ticodendron* and the families of Fagales offers positive evidence of relationship. Conceding a probable relationship between *Ticodendron* and Fagales, one must note the appreciably more primitive wood of *Ticodendron*. This accords with the rather primitive (compared to other Fagales) floral morphology of *Ticodendron* (Gómez-Laurito & Gómez P., 1989). *Ticodendron* can be considered a very primitive element in Fagales. It could not be included in any of the existing fagalean families without markedly altering the family description, with respect not only to wood anatomy but to other features as well (see other papers in this series). Therefore, wood and bark anatomy support placement of *Ticodendron* in a monogeneric family referred to Fagales. Wood and bark of other families considered earlier in discussions among the authors of other papers on *Ticodendron* were considered in comparisons: Brunelliaceae, Dilleniaceae, Juglandaceae, Myricaceae, Picrodendraceae, and *Nothofagus* (which several authors now segregate from Fagaceae). The anatomical resemblances between *Ticodendron* and these families are appreciably fewer than the resemblances between *Ticodendron* and Betulaceae and Corylaceae (or Coryleae of Betulaceae), and so such comparisons have been omitted.

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THE LEAF ARCHITECTURE OF *TICODENDRON* AND THE APPLICATION OF FOLIAR CHARACTERS IN DISCERNING ITS RELATIONSHIPS[1]

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ABSTRACT

Leaves of the recently described genus *Ticodendron* are simple, alternate, stipulate, symmetrical, elliptical with attenuate apices and acute bases, a single order of serrations representing modified rosid teeth, pinnate, craspedodromous principal venation, percurrent tertiaries, well-developed, random areolation, anomocytic stomates, and T-shaped hairs. Phenetic and cladistic analyses of leaf and other characters of *Ticodendron* were performed in order to determine its affinities and evolutionary relationships. Several new characters, including the number of veins joining the midrib and the venation of the marginal teeth, were added to the suite of standard leaf architectural descriptors because of their demonstrated potential as systematic indicators. After filtering out nonapplicable and symplesiomorphous characters, a total of 70 characters (48 leaf and 22 reproductive and wood) remained. These were organized into two main data sets, with the second further divided to form three subsets, which were then analyzed using a simple similarity comparison and parsimony methods. From the standpoint of its gross phenetic and phylogenetic affinities, *Ticodendron* belongs to a group of amentiferous taxa, with the extinct genus *Fagopsis* showing the strongest affinity, followed by *Brunellia*, *Castanopsis*, *Castanea*, *Alnus*, and *Nothofagus*. Our cladistic analyses show *Ticodendron* grouping with the Fagales and occasionally with the Myricaceae in a rosalean clade whose base is embedded in the Cunoniaceae. These data support recognition of the new genus as a member of a distinct family in the order Fagales and with closest affinities to Fagaceae and Betulaceae.

The recent discovery of a relatively common tree of unknown affinities in middle elevation, wet primary forests of Panama and Costa Rica is vivid evidence of what is being lost as the deforestation of the tropics continues.

Determining the systematic affinities of *Ticodendron* Gómez-Laurito & Gómez P. is especially challenging because it has a mosaic of characters that defy ready placement. Its general affinity is with the more derived members of the highly unnatural group of dicotyledons with reduced flowers (Behnke, 1989; Thorne, 1989; Wolfe, 1989) known as the Amentiferae. Thus, during the exchanges by the working group, evidence has been cited for relationships to families as disparate as the Euphorbiaceae, Dilleniaceae, Juglandaceae, Betulaceae, and Ulmaceae. However, detailed anatomical and morphological investigations by members of the group are beginning to provide reliable characters. A consensus has developed that the affinities of *Ticodendron* lie near a group of amentiferous families that comprise the Hamamelidae of Cronquist and that include the Fagaceae, Betulaceae, Myricaceae, and possibly Juglandaceae.

The main objectives of this paper are to provide a concise and rigorous description of the leaves of *Ticodendron* and an assessment of its affinities, with an emphasis on foliar characters. We will also examine its phylogenetic relationships based on leaf and other characters assisted by cladistic techniques. Throughout, we will attempt to show the concordance between inferences of relationship that arise from an analysis of leaf characters with those of other organs. Our focus on leaves is based on the fact that they are morphologically complex organs, with a diversity of characters such as teeth and detailed venation patterns that often indicate phylogenetic affinity (Hickey & Wolfe, 1975). However, precisely because it now appears that certain elements of leaf architecture are congruent

[1] The assistance of Barry Hammel in coordinating this project and of MO in supplying specimens is gratefully acknowledged. The authors also thank Patricia Holmgren of the New York Botanical Garden for allowing preparation of certain leaf material, Xiaobo Yu of YU for preparing the slides, and members of the research group studying this plant for sharing their preliminary data.

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with systematic affinity at higher taxonomic levels, it is essential that more rigorous and explicit techniques of phylogenetic analysis be applied to lower taxonomic levels of the angiosperms in order to demonstrate the utility of leaf characters.

A number of such test cases already exist or are being developed. Levin (1986a, b, c) explicitly studied the correlation between the relationships based on leaf characters with phylogenies based on traditional characters within the Euphorbiaceae, a notoriously difficult family. The phenetic and cladistic results not only show the similarity between leaf and other data sets, but also suggest that the leaf data may be superior in some cases. Levin now plans to extend this survey to the Flacourtiaceae (pers. comm.). More recently, Todzia & Keating (in press) used foliar characters to distinguish clades in the Chloranthaceae where reproductive characters had provided ambiguous results. So has Hershkovitz (1988), who reported that such leaf architectural characters as vein course and leaf rank prove useful in the systematic interpretation of the Centrospermae, a group whose predominantly herbaceous character might lead to an inference of a high degree of leaf architectural plasticity and attendant homoplasy. Finally, Miller & Nowicke (1990) have used leaf architectural characters, in conjunction with a suite of other characters, to show the relationships of two genera in Boraginaceae.

At the present time, this and other evidence suggest that leaves may well provide information on phylogenetic relationships that is at least equal to that derived from any other organ or data set in the plant. Thus, although the major purpose of this study is to describe and elucidate the relationships of *Ticodendron*, we also hope to show that cladograms based on leaf characters are similar to those derived from other organs. To optimize our use of leaf characters, we refined and extended many of their definitions, such as tooth type, so that they would be more useful in distinguishing entities and in pointing to relationships at lower taxonomic levels. This increased the general robustness and utility of our leaf characters as well as elucidated the relationships of *Ticodendron* itself.

Materials and Methods

Cleared leaves of *Ticodendron* were prepared for this study from two specimens supplied by MO. These were prepared by the methods outlined in Hickey (1979) and Hickey & Wolfe (1975). Comparisons were made using the cleared leaves found in the National Cleared Leaf Collection (NCLC) housed at Yale Peabody Museum (YPM). Additional vegetative characters as well as the reproductive characters used were obtained by study of herbarium specimens housed at YU and NY or by recourse to the literature of systematic and comparative botany. A list of taxa examined, both from cleared leaves and herbarium specimens, appears in Table 1.

After a broad search of the National Cleared Leaf Collection at Yale University, 18 operational taxonomic units (OTUs) at the generic level from eight families (Table 1) were selected for detailed comparison to *Ticodendron*. This group included representatives from five amentiferous families, namely species of *Castanea*, *Castanopsis*, *Nothofagus*, the extinct genus *Fagopsis* (Fagaceae), *Alnus* (Betulaceae), *Pterocarya*, *Platycarya* (Juglandaceae), *Canacomyrica*, *Myrica* (Myricaceae), and *Rhoiptelea* (Rhoipteleaceae). In addition, several clades from three putatively primitive families of Rosales were examined. These included *Brunellia* (Brunelliaceae); *Davidsonia* (Davidsoniaceae); and *Acsmithia*, *Ceratopetalum*, and *Cunonia* (as representatives of Cunoniaceae). The genera of Cunoniaceae were chosen due to their apparently primitive phylogenetic position within the family based on leaf, reproductive, and wood characters (Dickison, 1980b) and general similarity to *Ticodendron*.

Formulation of a list of characters and character states that adequately described the leaf architecture of *Ticodendron* and allowed its comparison with other taxa was a crucial aspect of this analysis. Our starting point was the outline of leaf architectural characters established by Hickey (1979). As we collected data we found other overlooked characters that proved to have potential value in determining relationships. This led to an expansion in the terminological base, especially for characters that deal with tooth morphology and marginal venation (see Results below).

Initially, 71 vegetative characters were collected from cleared leaves and herbarium specimens. These included leaf architectural as well as node, stipule, cuticular, and twig features. In addition, seven wood characters and 17 floral and pollen characters were obtained from the working group and the literature (Gómez-Laurito & Gómez P., 1989; Carlquist, 1991; Feuer, 1991; Tobe, 1991). The high degree of similarity that characterizes the pollen of many of these OTUs (Batten, 1989) has been suggested to be a shared derived character for some groups of families in the Hamamelidae (Muller, 1984).

TABLE 1. List of species, OTU abbreviation, and collection information for the specimens used to generate the leaf architectural and other vegetational data used in this study. Fossil collections: YPM—Yale Peabody Catalogue for Fossil Plants; YPM-PU—Peabody Coll. ex Princeton Univ. Paleobotanical Coll.

Genus (family)	OTU	Source of leaf architectural characters	Source of other vegetative characters
Ticodendron (unknown)	TICO	*T. incognitum* (*Hammel, Bello, Haber, Kinsman & Lierheimer 15285*, YU), (NCLC 6383) *T. incognitum* (*McPherson 8401*, YU ex MO), (NCLC 6765)	same
Fagopsis (fossil) (Fagaceae)	FAGO	*F. longifolia* YPM 25404, 25467; YPM-PU 9809	same
Brunellia (Brunelliaceae)	BRUN	*B. colombiana* (*Cuatrecacas & Llano 27314*, US), (NCLC 3186) *B. racemifera* (*Barclay et al. 3413*, US), (NCLC 3190)	*B. comocladifolia* (*Wright 1133*, YU)
Acsmithia (Cunoniaceae)	ACSM	*A. densiflora* (*Hickey 5274*, YU), (NCLC 6545)	same
Ceratopetalum (Cunoniaceae)	CERA	*C. gummiferum* (*Wilkes s.n.*, YU), (NCLC 6713)	same
Cunonia (Cunoniaceae)	CUNO	*C. capensis* (*Cummings 300*, US), (NCLC 3165)	*C.* cf. *deplanchei* (*Hickey 5252*, YU)
Davidsonia (Davidsoniaceae)	DAVI	*D. puriens* (*Cronquist 11622*, NY), (NCLC 6766)	
Pterocarya (Juglandaceae)	PTER	*P. stenocarpa* (*Hickey s.n.*, YU), (NCLC 3220)	*P. caucasia* (*Brewer s.n.*, YU)
Platycarya (Juglandaceae)	PLAT	*P. strobilacea* (*Chen 3706*, GH), (NCLC 7001) *P. strobilacea* (*1757053*, US), (NCLC 410)	*Englehardtia spicata* (*Merrill 253*, YU)
Rhoiptelea (Rhoipteleaceae)	RHOI	*R. chiliantha* (*1577640*, US), (NCLC 804)	none
Canacomyrica (Myricaceae)	CANA	*C. monticola* (*Hickey 5210*, YU), (NCLC 6768)	same
Myrica (Myricaceae)	MYRI	*M. cerifera* (*358864*, US), (NCLC 143) *M. californica* (*E. Hall 468*, YU), (NCLC 6781)	*M. cerifera* (*Curtiss 2606*, YU)
Castanopsis (Fagaceae)	CAOP	*C. concolor* (*Schoh 101*, US), (NCLC 627)	*C. chrysophylla* (*E.W. Hammond 346*, YU)
Castanea (Fagaceae)	CAST	*C. pumila* (*Kearney, Jr. 892*, US), (NCLC 6136)	*C. dentata* (*Godfrey s.n.*, YU)
Nothofagus (Fagaceae)	NOH1	*N. discoidea* (*Baumann-Bodenheim 15111*, US), (NCLC 221)	*N. balansea* (*Hickey s.n.*, YU)
Nothofagus (Fagaceae)	NOH2	*N. fusca* (*Walker 4696*, US), (NCLC 1765) *N. moorei* (ex Herb. Melbourne *s.n.*, US), (NCLC 55)	*N. balansea* (*Hickey s.n.*, YU)
Alnus (Betulaceae)	ALN1	*A. nepalensis* (*Stibolt s.n.*, US), (NCLC 5387)	*A. crispa* (*A. Hill 2541*, YU)
Alnus (Betulaceae)	ALN2	*A. rhombifolia* (*Plaskett s.n.*, US), (NCLC 5402)	*A. crispa* (*A. Hill 2541*, YU)

Several operational difficulties were encountered in coding the tooth characters. Problems included the existence of two different types of teeth (cunonioid and rosid; Hickey & Wolfe, 1975) on the same leaf, and in rare cases transitional forms, both in the same species and in closely related taxa, that lay morphologically between the common basic teeth types (e.g., in Juglandaceae, *Rhoiptelea*, *Davidsonia*, and Myricaceae).

Each tooth type can be described by a suite of characters (see below, Fig. 2). To describe two tooth types in a single taxon, it is necessary to have two sets of descriptive tooth characters, one for each type. Thus tooth type 1 (cunonioid) is

coded by characters 6–11 and type 2 (rosid) by characters 12–17 and 20. This created a problem when an OTU had only one tooth type. Normally, if a character is missing, it is either coded as unknown, which allows computerized cladistic algorithms to assign an optimal state, or coded as a single character state for the absence of the character. Yet if an entire tooth is missing, in the second case each state of the entire suite of characters is coded as absent, and these states could act as shared derived characters for a group of taxa. Yet the absence of these characters could be due to parallel loss, the ancestral condition (thus are symplesiomorphies), or actual shared derived states. This presents difficulties for our analysis because the lack of rosid teeth is also ancestral, based on outgroup comparison. Our solution was to code each of the characters of the missing tooth type as a nonapplicable state (NA) in the cases where only one tooth type existed. We created an NA state for each family where at least one OTU was lacking a tooth type. We suggest that this method results in underweighting of these characters (they are either autapomorphies or synapomorphies at the top of the tree), but at least avoids grouping taxa based on symplesiomorphies or on less secure character loss states.

In order for our analysis to deal with OTUs having transitional teeth, we chose to use the most fully developed extreme of each of the two tooth types. In fact, in a given OTU these extremes tended to be the most common.

Once the matrix was formed, we found a number of characters, particularly of the leaf, that proved to be inappropriate at the level we were using them. They were removed if they either did not vary at the taxonomic level being examined or if they were polymorphic at the generic level and thus only useful for elucidating specific relationships. In addition, we removed all autapomorphic characters, characters in which many of the OTUs were missing data, and finally, a few characters that further study indicated were not structurally homologous.

The remaining 70 characters (48 leaf and 22 reproductive and wood) were used in our phylogenetic analysis (Appendix). Some OTUs had multiple character states for specific characters (the states not used in the analysis are provided at the end of the description of each character in the Appendix). Since the version of PAUP we used to implement our cladistic analysis can only use one state for each OTU, we had to devise an objective protocol in order to decide which character states to include for a given OTU. For an OTU, if a character was polymorphic and shared a state with *Ticodendron*, we chose that state because the principal objective of this analysis was to ascertain the affinities of *Ticodendron*. If none of the states were the same as those of *Ticodendron*, the state that was most common in the OTU was chosen. If all states were equally common, the state most common for all of the OTUs was used. If none of the states were similar to the most common state, we used the state most similar to that of a closely related taxon. Finally, if two closely related taxa (same family or genus) shared two character states, each OTU was assigned a different state.

The resulting data matrix was arranged to form two sets (Tables 2, 3), with the second set divided into two additional subsets (characters 1–48 and 49–70). The first set (Table 2) included all 18 OTUs and the vegetative characters, excluding wood (characters 1–48). To compare vegetative and other data sets it was necessary to reduce the number of OTUs because data on reproductive and wood morphology were missing for several of the OTUs, or were the same for *Nothofagus*2 and *Alnus*2. Thus, our second data set (Table 3) had 14 OTUs and 70 characters. Two types of analyses were performed on each of the two data sets. First was a simple similarity comparison, whose similarity coefficient was calculated by counting the number of character states shared by *Ticodendron* and each OTU and dividing it by the number of known characters. The remaining analyses were based on synapomorphy and parsimony. Our phylogenetic analysis used the program PAUP (Swofford, 1985). The major options of this program that we used were global branch swapping, mulpars, and rooting to a hypothetical ancestor to find the shortest trees. Variable options were ordering of the characters with two or rarely three character states, the option to treat the characters as completely unordered (those characters which are ordered are indicated as such in the Appendix), and the initial addition of sequence either closest or simple. Lastly, if multiple parsimonious trees were found, the trees were combined to form strict consensus trees (Swofford, 1985). The specific choice of outgroups, construction of the hypothetical ancestor, the method of ordering, and the resulting trees are discussed in the Results section below.

Results

In the following description of the leaves of *Ticodendron* and analysis of its affinities, the terms used are from Hickey (1979) with the addition of the following new terms or clarification of previous ones:

TABLE 2. Input data matrix for data set 1. OTUs are identified in Table 1 and characters are described in the Appendix.

OTU	Characters
	111111111122222222223333333334444444444
	123456789012345678901234567890123456789012345678
1 HYPO	000000000000000000000000000000000000000000000000
2 TICO	110212233343536352052110010111121103113021203311
3 FAGO	110104454573544522142110O1?1112?111?????21213304
4 BRUN	010200000003436352162110O1??00220000110010103210000002330?000003130200
5 ACSM	100211001010000000021000000010020?000000000100060000000000000100200
6 CERA	000000025020000003000000000002101124100100003300020002020100001003020O
7 CUNO	000000025020000002100010010002020004?13000000000204000000000114002000O
8 DAVI	011301011003335351162100120113200200011000002200100?2220001204131202l0
9 PTER	011000010003336354161102220200121001112110012210114124210100135120021l
10 PLAT	011200000003336361162102220210220201112110000210114124210100135120121l
11 RHOI	011200000103436352162100110100110201104010000110214120000000011300021O
12 CANA	111100000103336350161102302302110001125100101100
13 MYRI	110400001003436460162102300301221001125220201100
14 CAOP	110015566683336352062200100011220001101221202312
15 CAST	110505566683336342060210100013220001101221003312
16 NOH1	110100100061221213022101001100221002111021010300
17 NOH2	111010001023436350152201001112221112101021213000
18 ALN1	111100001003335550131210010102211001102221000010
19 ALN2	111103342453343350141210010111211111102221213313

(1) *sinus*—an indentation in the margin of the leaf associated with a tooth or a lobe. Their identification is straightforward if they are angular, but shallow, rounded sinuses may grade imperceptibly into undulations of an entire margin. In such cases, sinuses may be recognized by measuring the maximum depth of the marginal indentation and comparing this with the distance to the apex of the closest tooth (Fig. 1). This is done by dropping a perpendicular (cd in Fig. 1) to the nadir of the indentation from a line (ab) connecting the apices of the adjacent teeth and comparing the length of this line with the distance (in this case ac) to the closest tooth. If the depth (cd) is greater than the distance to the closest tooth (ac or bc) the marginal indentation is a sinus, otherwise not.

TABLE 3. Data matrix for data set 2. OTUs are identified in Table 1 and characters are described in the Appendix.

OTU	Characters
	111111111122222222223333333333444444444455555555556666666667
	123456789012345678901234567890123456789012345678901234567890123456789O
1 HYPO	000000000000000000000000000000000000000000000000000000000000000000000000000000
2 TICO	110212233343536352052110010111121103113021203311214120000101121230111l
3 FAGO	110104454573544522142110O1?1112?111?????212133040050O????0111???011??
4 BRUN	010200000003436352162110O1??00220000110010103210000002330?000003130200
5 ACSM	100211001010000000021000000010020?000000000100060000000000000100200
6 CERA	000000025020000003000000000002101124100100003300020002020100001003020O
7 CUNO	000000025020000002100010010002020004?13000000000204000000000114002000O
8 DAVI	011301011003335351162100120113200200011000002200100?2220001204131202l0
9 PTER	011000010003336354161102220200121001112110012210114124210100135120021l
10 PLAT	011200000003336361162102220210220201112110000210114124210100135120121l
11 RHOI	011200000103436352162100110100110201104010000110214120000000011300021O
12 MYRI	110400001003436460162102300301221001125220201100114120200100115121121l
13 CAST	110505566683336342060210100013220001101221003312003013101?000033020211
14 NOH1	110100100061221213022101001100221002111021010300211103301?0111?2401211
15 ALN1	111100001003335550131210010102211001102221000010214110102?01111240121l

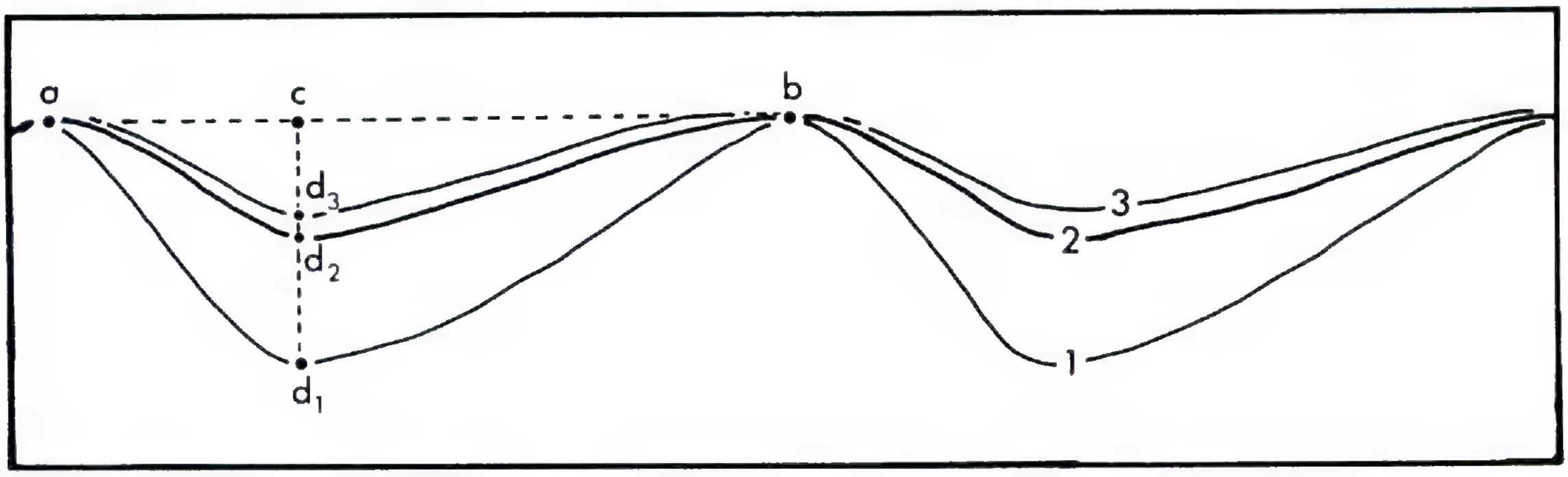


FIGURE 1. Determination of the presence of a sinus between teeth in three different marginal configurations (labeled 1, 2, and 3) where the nadir of the indentation is rounded. Tooth apices lie at points a and b, with d indicating the nadir of the sinus (in the case of d_1) or of the marginal indentation (d_2 and d_3). Where cd > ac or cb the indentation is a sinus; where cd < ac or cb the indentation is not.

In the course of this work we found it necessary to elaborate upon the terminology available to describe the types of venation and vein courses at the margin and especially within the teeth of the leaf. The complete list of character states for these appear in the Appendix, but we give definitions for several of the most important characters below because of their importance in our analysis.

The first set of these are the veins associated with the teeth. These begin with:

(2) the *principal vein*—the thickest vein found within the confines of the tooth (Fig. 2, P). This is followed by:

(3) the *admedial vein*—the first branch from the principal vein below the tooth apex on the admedial side of the tooth (if from a tooth located at the leaf apex, then the first branch from either side of the principal vein that has the subsequent characters) that is the same, or one vein order lower than the principal vein, is distal to any exmedial vein of similar strength, and has > 60% of its vascular tissue at its junction with the principal directed away from the tooth apex (Fig. 2, Ad).

(4) *accessory veins*—collectively, all the veins between the tooth apex and the admedial vein that either branch from or merge with the principal vein including the *conjunctal* veins (defined below) (Fig. 2, Ac).

(5) *conjunctal veins*—accessory veins of the tooth that converge upon or merge with the principal vein and contribute vascular tissue to the tooth apex. Conjunctal veins must have at least 60% of their vascular tissue directed toward the tooth apex at their point of convergence or fusion with the principal vein. They may occur in pairs, arising either oppositely or alternately to one another, or they may be single (Fig. 2, C).

(6) *comb vein*—an admedial branch of a secondary vein, arising near the margin and running along it, from which originate several tertiary veins that run admedially to the superadjacent secondary vein (Fig. 5, C). They occur singly or sometimes as an inner and an outer comb vein.

In an unpublished survey of angiosperm venation, we have noted that the number and configuration of the different classes of veins arising from the midvein of the leaf have proven to be of considerable value in determining affinity. Because the categories of veins used in this analysis carry an inference of evolutionary homology, we felt that a new set of terms was necessary to distinguish them from venation terms such as secondary, tertiary, and intersecondary in the system of Hickey (1979) where categories are recognized strictly on the basis of similarity in course and size where they attach to the midvein. These new terms are as follows:

(7) *deuteral veins*—consisting of the secondary veins of a leaf, the midveins of lateral leaflets, lateral primaries, and all those secondaries of the

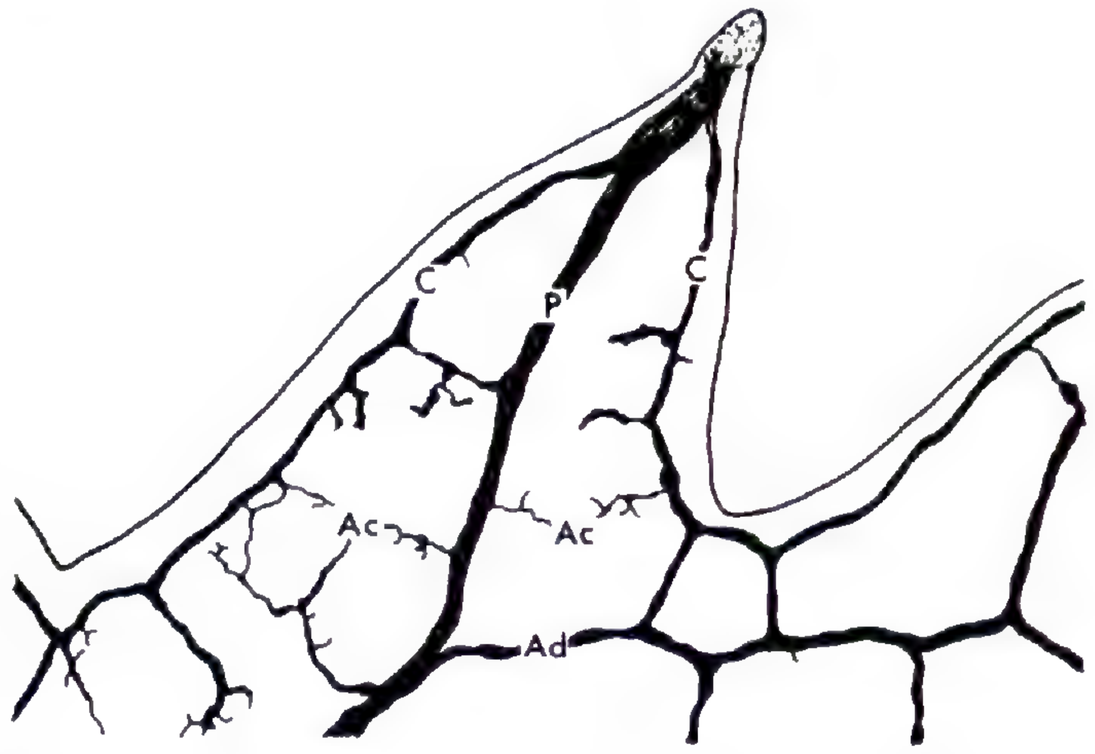


FIGURE 2. An ideal tooth with the major types of venation labeled. Ac—accessory veins, Ad—admedial vein, C—conjunctal veins, P—principal vein.

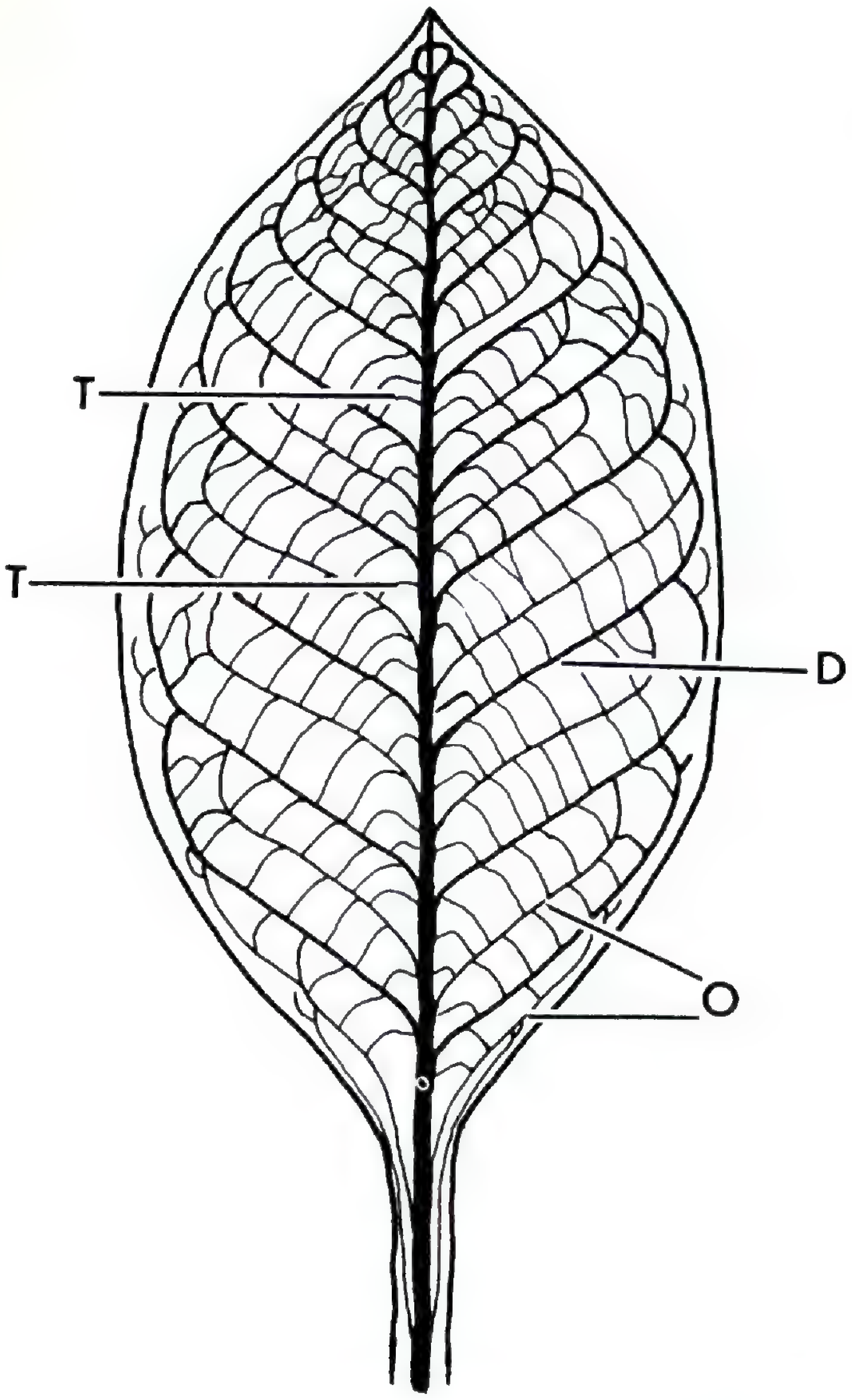


FIGURE 3. Venation of a simple leaf showing the deuteral (D), opadial (O), and trinal (T) veins.

same size-class or whose size is part of a smooth gradation of sizes and whose behavior does not differ markedly from the majority of secondaries (Fig. 3, D).

(8) *opadial veins*—comprising the intersecondaries and those secondaries of abruptly different size and behavior from the majority of the secondaries (Fig. 3, O).

(9) *trinal veins*—the next thinnest vein set consisting of those tertiary veins that connect to the midrib and which arise either from secondary veins or from intersecondaries (Fig. 3, T). The sum of these three vein sets will be designated as the D-O-T veins collectively.

A final addition to the original set of leaf architectural terms involves a new term for the configuration of the marginal ultimate venation, as follows:

(10) *spiked*—margin with short, outward-pointing ultimate veins that are either unbranched or with a single pair of short branches (Fig. 4).

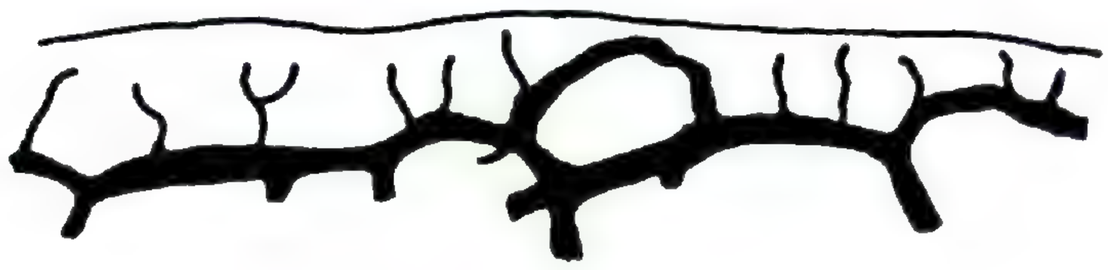


FIGURE 4. Spiked marginal ultimate venation.

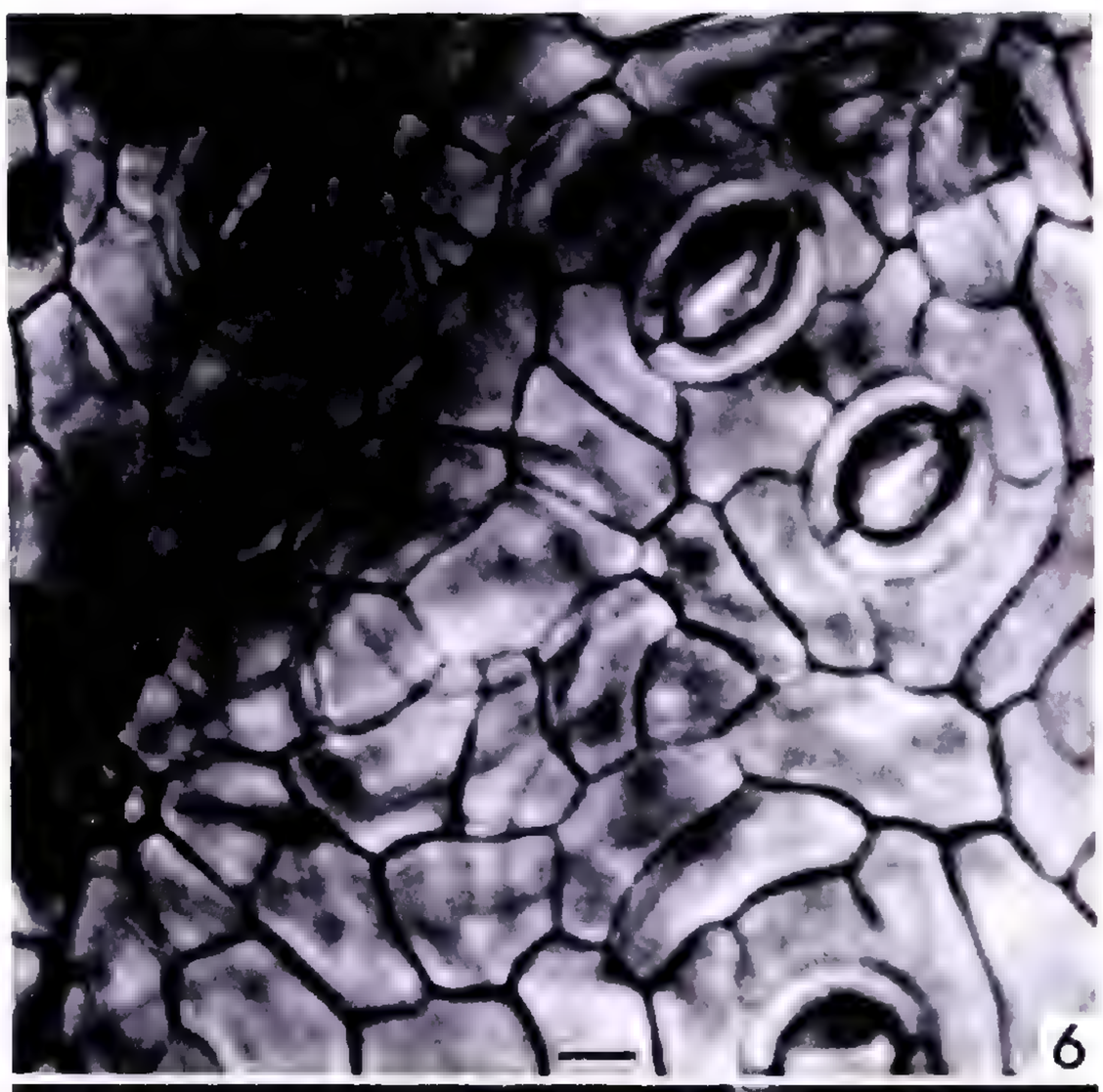
LEAF ARCHITECTURAL DESCRIPTION OF *TICODENDRON INCOGNITUM*

Leaves alternate with encircling bases, stipulate with deciduous stipules attached to a ridge of petiolar tissue that extends transversely from the sides of the enlarged and raised site of leaf attachment (Fig. 7). Stipules completely encircling the apical and axillary buds. Leaf abscission scars with three traces, lacunae 3. Leaf simple, symmetrical, except slightly asymmetrical at the base; shape elliptical with a length to width (l/w) ratio of from 1.8 to 2.8 (mean 2.1, standard deviation 0.2, N = 15). Apex attenuate, base acute, texture chartaceous (Fig. 5).

The leaf margin is serrate in a single order with from 5 to 12 teeth (mean = 11) per side; generally there is one tooth per secondary vein with an average spacing in mature leaves of 1.3 cm. Serrations concave on their apical and basal sides (type C3) and have elongate, abaxially directed, soon deciduous, glandular tylate processes (a capitate pad of clear glandular tissue at the tooth apex; Fig. 8). The principal vein of the serration is medial and represents the continuation of a secondary vein that enters the serration straight and is then deflected slightly downward (Fig. 5). Principal vein termination tapered to abrupt, the principal accompanied by an admedial vein and at least one admedial conjunctal vein with accessory branches on its inner margin (Fig. 18). Conjunctal veins in opposite pairs when both are present. The presence of a medial principal vein and conjunctals on both sides of the principal in a tooth of this morphology implies that *Ticodendron* possesses modified rosid teeth in the classification of Hickey & Wolfe (1975). The sinuses between the teeth are rounded and unbraced but are approached by a conjunctal vein or a branch from the conjunctal.

Venation pinnate, craspedodromous (Fig. 5). Secondaries diverge at a moderate acute angle (45–60°) and have a uniform spacing and angle of divergence. Secondaries slightly recurved and unbranched until they reach the base of the serration where they give off a comb vein, that is, a branch that runs close to the margin while giving off several tertiary veins to the superadjacent secondary (see

5



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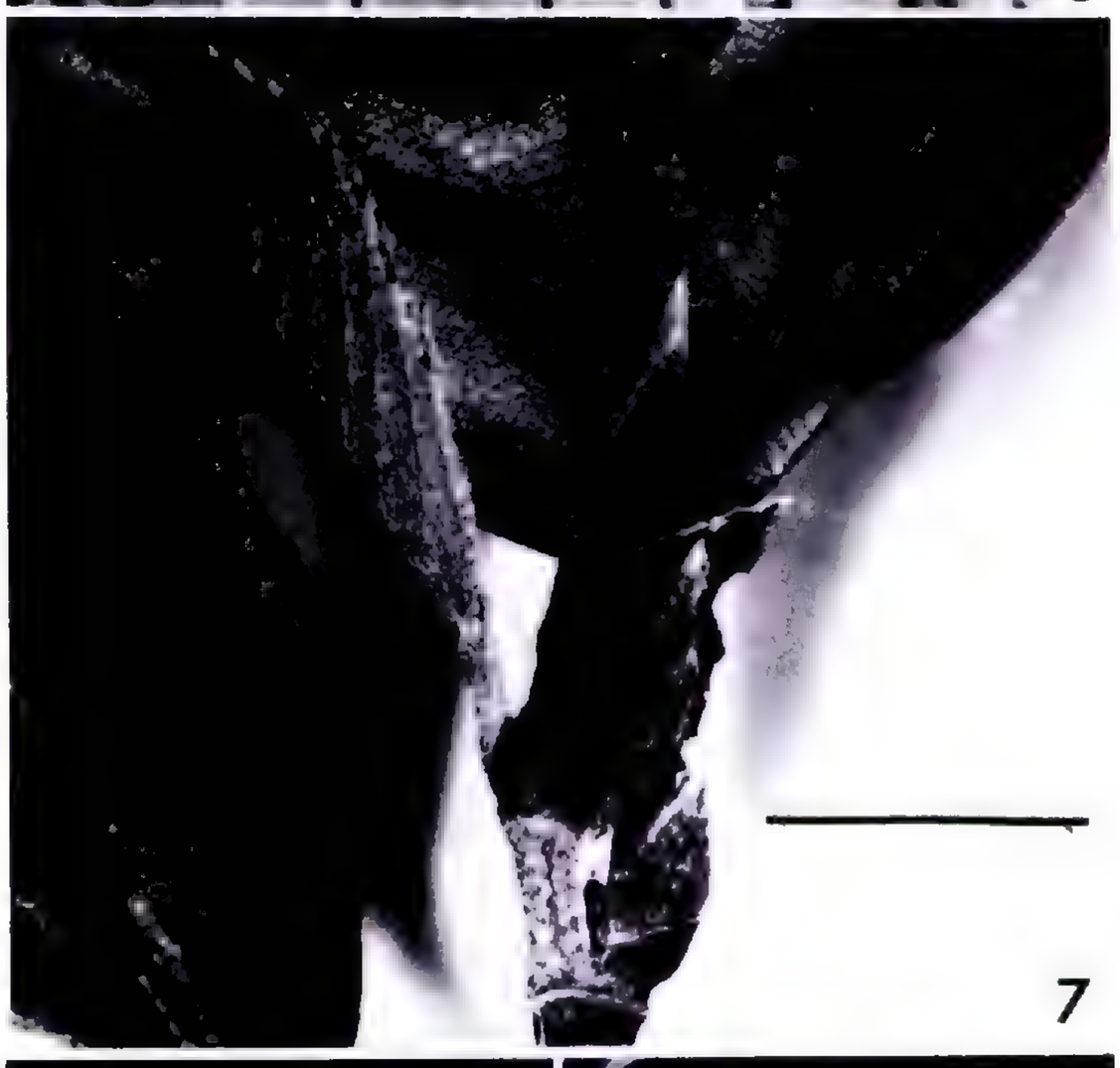

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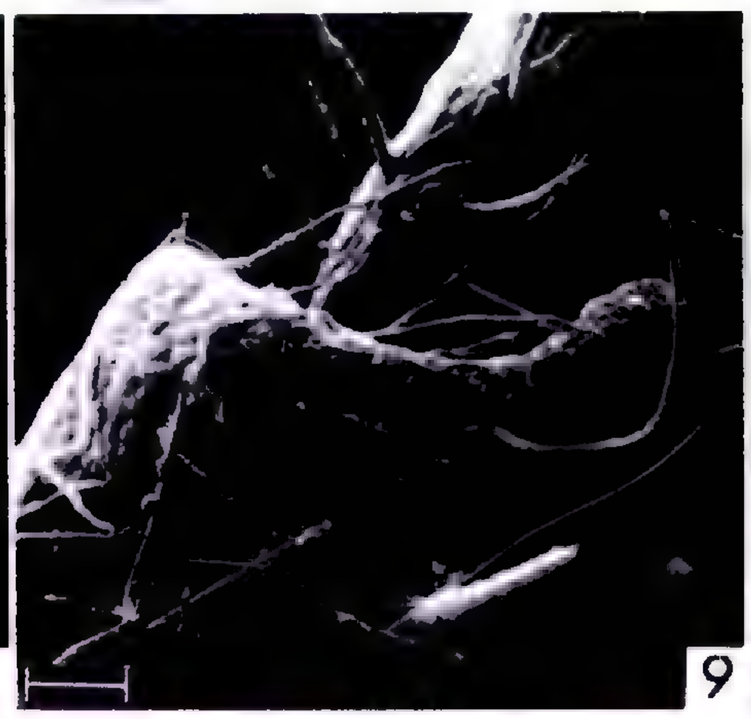

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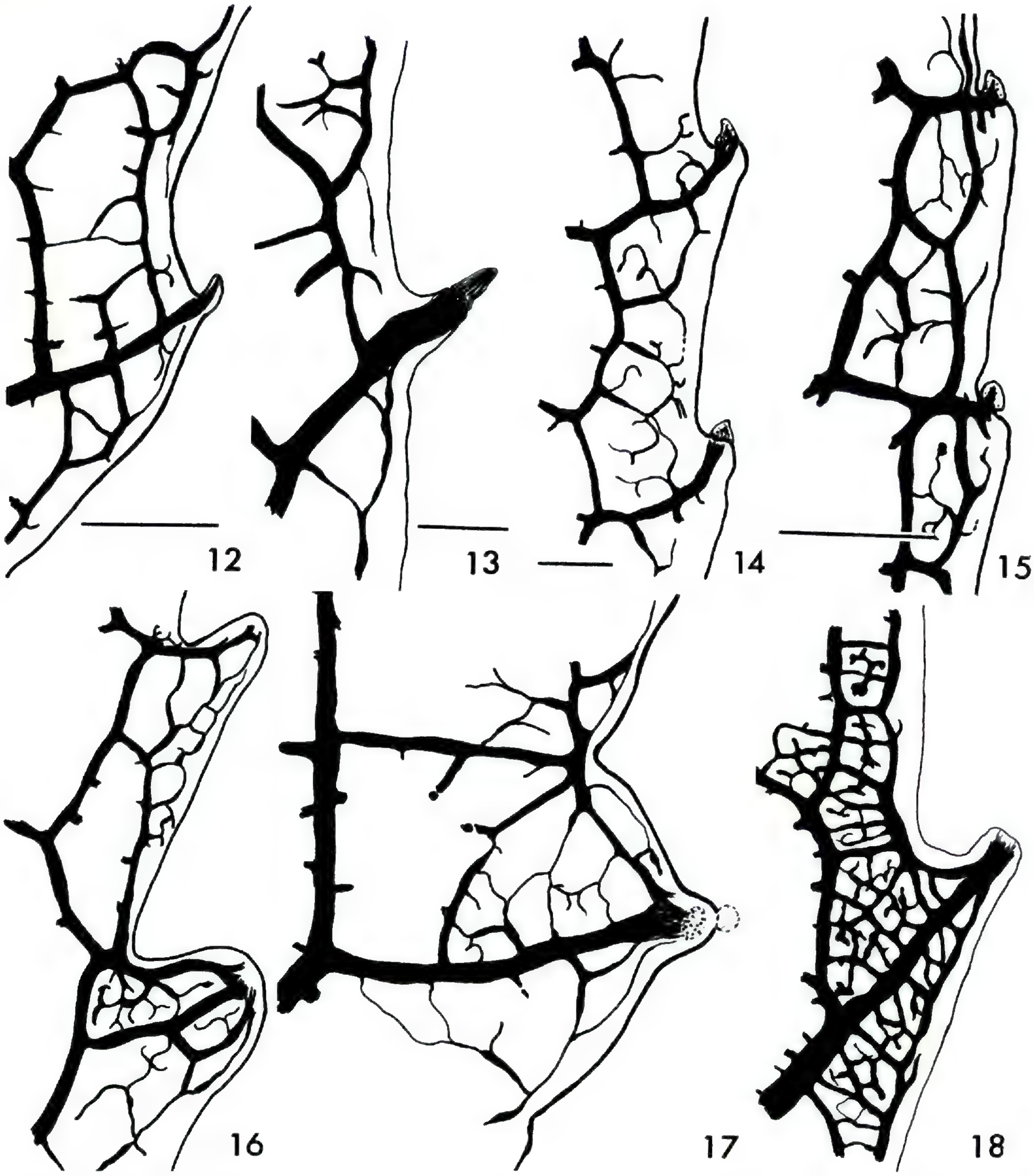
10

11

FIGURES 5–11. Details of leaf characters. 5–8. *Ticodendron incognitum* (*Hammel et al. 15285*, YU).—5. Whole cleared leaf. c—comb vein (NCLC 6383). Scale bar = 10 mm.—6. Lower cuticle showing hair base and stomatal anomocytic complexes (NCLC 6383). Scale bar = 100 μm (0.1 mm).—7. Apical portion of woody twig. Note the large stipules that encircle the axes, and in the node below, the circular scar that remains on the axis. Scale bar = 10 mm.—8. Scanning electron microscope (SEM) view of a tooth of an unexpanded leaf; note the elongate process at its apex. Scale bar = 100 μm (0.1 mm).—9. *Davidsonia puriens*, tooth of a young leaf with an elongate, slightly bulbous process near its apex (*Cronquist 11622*, NY). Scale bar = 100 μm (0.1 mm).—10. *Castanea* dentata, young tooth with apical, capitate process (*Nichols s.n.*, YU). Scale bar = 10 μm (0.01 mm).—11. *Corylus americana*, young tooth with a short, apical, deciduous process (*Nichols s.n.*, YU). Scale bar = 10 μm (0.01 mm).



FIGURES 12–18. Camera lucida drawings of teeth from cleared leaves.—12. A typical dillenioid tooth from *Doliocarpus dentatus* (Dilleniaceae) (*Bartlett 11367*, US) (NCLC 857).—13. A tooth of *Tetracera volubilis* (Dilleniaceae) with the typical dillenioid-type architecture but with a deciduous process (*Gentle 3363*, US) (NCLC 828).—14. A typical theoid tooth from *Hartia sinensis* (*239672*, US) (NCLC 5).—15. Tooth of *Ceratopetalum gummiferum* (Cunoniaceae), which has many similarities to the theoid tooth in 14 (*Wilkes s.n.*, YU) (NCLC 6713).—16. Two dimorphic teeth of *Canacomyrica monticola* (Myricaceae). The upper tooth is a typical cunonioid tooth while the lower is a rosid tooth. Note the asymmetrical venation in the lower tooth (*Hickey 5210*, YU) (NCLC 5210).—17. A typical rosid tooth from *Alnus nepalensis*. Note the asymmetrical venation in the tooth and the sometimes deciduous apical tip (*Stibolt s.n.*, US) (NCLC 5387).—18. A tooth of *Ticodendron incognitum*. Note the similarities to the teeth in 16 and 17 indicating that it is a rosid tooth (*McPherson 8401*, YU ex MO) (NCLC 6765). All scale bars 1 mm. Figure 16 same magnification as 14, 17 same as 15, and 18 same as 13.

TABLE 4. Table of the similarity of *Ticodendron* to other OTUs in each data set. These figures are calculated from the number of shared characters divided by the number of characters known for each OTU. OTUs are identified in Table 1.

	Data set 1	Data set 2		
	(leaf characters)	a (all characters)	b (leaf characters)	c (reproductive & wood)
FAGO	0.537	0.491	0.537	0.500
BRUN	0.500	0.373	0.500	0.095
ACSM	0.319	0.304	0.319	0.273
CERA	0.250	0.243	0.250	0.227
CUNO	0.277	0.304	0.277	0.364
DAVI	0.312	0.290	0.312	0.238
PTER	0.312	0.371	0.312	0.500
PLAT	0.333	0.400	0.333	0.545
RHOI	0.417	0.471	0.417	0.590
CANA	0.250	NA	NA	NA
MYRI	0.354	0.429	0.354	0.591
CAOP	0.521	NA	NA	NA
CAST	0.458	0.377	0.458	0.190
NOH1	0.354	0.426	0.354	0.600
NOH2	0.458	NA	NA	NA
ALN1	0.375	0.478	0.375	0.714
ALN2	0.458	NA	NA	NA

C on Fig. 5). Secondaries in 5–11 pairs; intersecondary veins lacking.

Tertiary veins percurrent, opposite, closely spaced (> 0.5 mm); sigmoidally curved; exmedial angle of origin slightly acute to perpendicular (mean 85°, mode 90°); admedial angle displaying the highly unusual character of being markedly obtuse (mean 95°, mode 97°). Fourth-order veins strongly impressed, orthogonal; fifth order strongly impressed, generaly random; highest vein order fifth; marginal ultimate venation looped. Freely ending veinlets present, curved, mostly twice-branched. Areolation well developed, randomly oriented, mostly quadrangular, of medium size (mean diameter 0.6 mm); leaf rank (following Hickey, 1977) $3r^1$.

Upper epidermis with straight-sided cells and many radial arrays of cells as from a hair base. Lower epidermis with anomocytic (rarely approaching cyclocytic) stomates, guard cells with thickened polar walls and a highly distinctive annular thickening on their inner ledges (Fig. 6). Both epidermal surfaces, but most commonly the lower one, with what appear to be overthrust glands in pits formed by the projecting edges of the surrounding cells, which are sometimes aligned in radial arrays away from the pit. Trichomes very rare in the mature leaf, common in immature specimens (Fig. 8); T-shaped, no scales noted.

GROSS PHENETIC AND PHYLOGENETIC AFFINITIES

The similarity of the leaves of *Ticodendron* to our OTUs is given in Table 4. The combination of simple, craspedodromous leaves with a single tooth per secondary, angle of basal secondary origin the same as for the upper secondaries, an excess of 60 D-O-T veins; strongly percurrent, sinuous tertiary veins; with teeth having a tapered or abrupt, but not bulbous, termination; one or sometimes two pairs of conjunctal veins with inward-branching accessories; and the presence of marginal comb veins strongly suggests a group of taxa in the so-called Amentiferae, consisting of the Fagaceae including *Nothofagus*, Betulaceae, the fossil genus *Fagopsis*, and also the family Brunelliaceae (Rosales). In addition, the venation and marginal configuration of some pinnately compound leaves in the Juglandaceae and the Rhoipteleaceae warranted a more careful comparison to those families. Emphasis on the amentiferous group of genera is reinforced as well by the reduced flowers (Tobe, 1991) and the pollen (Feuer, 1991) found in *Ticodendron*.

Leaves of the extinct genus *Fagopsis*, with a similarity coefficient of 0.537 (Table 4), are most like those of *Ticodendron* even to the tapered terminal portion of the principal veins of its teeth. However, *Fagopsis* has convex-convex teeth (character 4) lacking conjunctal veins (16), angular sinuses (5), uniformly symmetrical leaf bases (47), well-developed areolation (31), and a deuteral-opadial-trinal (D-O-T) vein total of between 41 and 60 (35) as opposed to > 60 for *Ticodendron*.

Among living genera, *Brunellia*, *Castanopsis*, and *Castanea* have similarity coefficients (*s*) of 0.50, 0.521, and 0.458, respectively, and also share the character of having tapered terminations of the principal veins of their teeth. Furthermore, both *Castanea* and *Castanopsis* have rounded sinuses similar to those of *Ticodendron*. However, *Brunellia* has pinnately compound leaves (character 1) with angular sinuses and semicraspedodromous secondaries (29), while the two fagaceous genera have teeth with tylate processes (22), nondeciduous stipules (25) that are not attached to the expanded leaf base (26), more than 18 deuteral veins (33), and a total of deuteral and opadial veins that ranges between 18 and 28 (34). All three genera have well-developed areoles (31) and glandular peltate and simple trichomes (36).

Leaves of *Alnus* (s = 0.458 and 0.375) and

Nothofagus (s = 0.458 and 0.354) are similar to those of *Ticodendron* in their general shape and vein configuration. However, both genera lack the comb veins (character 44) found in *Ticodendron*, and most other genera of Rosidae examined have well-developed areoles (31), glandular peltate trichomes (*Nothofagus*) or both glandular peltate and simple ones (*Alnus*) (36), D-O-T vein numbers of between 41 and 60 (35), and splayed (*Alnus*) (Fig. 17) or truncate and splayed (*Nothofagus*) terminations to the principal veins of the teeth (18). *Alnus* differs further from *Ticodendron* in having two orders of convex-convex marginal teeth (4) with clear glandular (21), tylate (22) apices and splayed principal vein terminations (18) (Fig. 17). Additional differences between *Nothofagus* and *Ticodendron* include teeth of different shape (4), leaf bases that are always symmetrical (47), basal secondaries at a lower angle than those above (3), and petioles that have both wings and stipules attached (24) (see Tables 2, 3).

Among the remaining hamamelid genera examined in this study *Rhoiptelea* (s = 0.417), *Platycarya* (s = 0.333), and *Pterocarya* (s = 0.312) were dissimilar because of their pinnately compound leaves. Two genera of the Myricaceae, *Myrica* (s = 0.354) and *Canacomyrica* (s = 0.250), have simple leaves but these show numerous differences such as teeth of the wrong shape (character 4) (Fig. 16), angular rather than rounded sinuses (5), a lack of stipules (24), symmetrical leaf bases (47), glandular, peltate, and simple trichomes (36), and a D-O-T vein number of from 19 to 38 (34).

These data suggest that the affinities of *Ticodendron* are with amentiferous families with rosid teeth (Hickey & Wolfe, 1975) which, despite their inclusion in the subclass Hamamelidae in the classifications of both Takhtajan (1969) and Cronquist (1988), have leaf architecture that is indistinguishable from that of the subclass Rosidae (Hickey & Wolfe, 1975; Wolfe, 1989). These two groups also share other characters (Dickison, 1989). For these reasons we also examined several other families of Rosales that are regarded as representing the most primitive families in Rosidae.

Acsmithia (s = 0.319) is notable because it is the member of the Cunoniaceae with the highest level of similarity to *Ticodendron*. The genus has simple leaves with a single order of teeth (character 3) of the proper shape (4) and only of the rosid type. However, these teeth appear to be a less derived form of the rosid type than in *Ticodendron* because they possess a full set of accessory veins (8) and have splayed terminations. Other differences include opposite leaves (2) with semicraspedodromous venation (24) and paracytic stomates (37).

The above families form the basis of our cladistic analysis described below. In this, we used Cunoniaceae to polarize our characters. In Takhtajan's 1969 and 1980 classifications this family is thought to be the most primitive of his Saxifragales, the primitive order of Rosidae. Studies by Dickison (1975a, b, 1980a, b, 1984, 1989) have further strengthened the position of the Cunoniaceae. Cronquist (1988) also regarded the family as very primitive in the Rosales, although not the most ancestral. What is apparent for this family, like so many other truly primitive taxa, is the high degree of morphological variability to be found within it as well as the somewhat capricious expression of this variability (Dickison, 1989). Thus the family has, in some cases, tricolporoidate pollen (Hideux & Ferguson, 1976), extremely primitive wood (Dickison, 1977), and low- to moderate-rank leaves. Extreme variation is apparent in characters including the perianth, which varies from present to nearly absent, ovary position from hypogynous to epigynous, the frequent occurrence of a nectariferous disk surrounding the carpels (Dickison, 1984), and the presence of both simple and compound leaves within the same genus, such as *Weinmannia*. Cunoniaceae are especially variable in their carpellary morphology, which ranges from follicles to capsules and even drupes. Superficially the family runs nearly the whole gamut of diverse fruit types seen in the Rosidae and the Amentiferae, even to configurations seen in *Liquidambar* (*Pancheria*), *Staphelia* (*Gillbeea*), and *Pterocarya* (*Ceratopetalum*) (Dickison, 1984).

In addition, a number of fused, bicarpellate follicles with two stigmas or stigmas that approach fusion into a single bifid structure and whose flowers have highly reduced perianth are found in the genus *Acsmithia* and in the satellite family Davidsoniaceae (Dickison, 1984; Cronquist, 1981).

Cronquist (1988) has commented on the difficulty of distinguishing the Cunoniaceae and other Rosales from Dilleniidae. We uncovered a striking instance of this transitional position when we found marginal teeth in the leaves of the Australian genera *Ceratopetalum* and *Aphanopetalum* that closely resembled the theoid type found in the moderately derived Dilleniidae (Fig. 15 and compare to 14). Thus, the transformation to the cunonioid tooth type found in the Rosales and the amentiferous taxa discussed here must occur within the Cunoniaceae because both occur there.

Nothing closely resembling the rosid tooth type

TABLE 5. Comparison between data sets and different options. The options are addition of sequence = closest (closest), addition of sequence = simple (simple), unordered in part (part), and unordered all (all). Data set 1 included characters 1–48 and 18 OTUs, and data set 2 included all or parts of characters 1–70 and 14 OTUs.

Data set options	Number of trees	Length of trees	Consistency index
Data set 1			
Closest part	2	260	0.527
Simple part	2	260	0.527
Closest all	1	249	0.550
Simple all	15	250	0.548
Data set 2			
All characters			
Closest part	3	305	0.587
Simple part	3	305	0.587
Closest all	1	295	0.607
Simple all	2	294	0.609
Characters 1–48			
Closest part	1	213	0.601
Simple part	1	213	0.601
Closest all	9	204	0.627
Simple all	9	204	0.627
Characters 49–70			
Closest part	3	75	0.680
Simple part	3	75	0.680
Closest all	3	74	0.689
Simple all	3	74	0.689

with its frayed termination of the principal vein and conjunctals with inner branches occurs anywhere in the subclass Dilleniidae. Several genera of the family Dilleniaceae, including *Dillenia* and *Doliocarpus*, resemble *Ticodendron* in form, secondary venation, and strongly percurrent tertiaries (Wolfe, 1989). Their teeth (Figs. 12, 13), in contrast to *Ticodendron*, have the slightly bulbous termination of their principal veins that characterizes the dillenioid tooth type (Hickey & Wolfe, 1975), and lack conjunctals with inner branches and the comb veins that characterize many members of Rosidae. For this reason our search was limited to the Rosidae and Amentiferae.

EVOLUTIONARY ANALYSIS

Our evolutionary analysis of the relationships of *Ticodendron* progressed through a number of methodological stages, roughly along the lines suggested by Eldredge (1979) and Neff (1986). The first and potentially most important of these stages was character analysis (Kaplan, 1984; Neff, 1986; Stevens, 1987; Steele et al., 1988). At this stage features are described, characters and character states are defined, and useful characters are selected. This is followed by character polarization in which ancestral states and structural transition series are identified. These characters and their polarized states are then used in the next stage. For this we used pattern sequence analysis to identify the optimal branching patterns. The last stage is systematic analysis, which uses a variety of data to identify the evolutionary relationships of the taxa.

We paid particular attention to character analysis during this research. Such an analysis produced a matrix showing the distribution of character states that are hypothesized to be structurally homologous. During this stage we made no attempt to equate structural homologies with evolutionary homologies. We considered that if the same character state is found in different taxa it is fundamentally similar in structure. We feel that our explicit terminology and rigorously defined character states facilitated our recognition of structurally similar features. In the Appendix, these characters are defined by topological, anatomical, or morphological similarity, while the states are distinguished by more subtle differences.

When assigning polarities to character states we hypothesized the ancestral states and the transitions between them using outgroup comparison (Maddison et al., 1984). Because we consider *Ticodendron* to be a member of Rosidae, for the reasons given above, we chose as our outgroup the family Cunoniaceae, which we consider to be primitive in the subclass.

The occurrence of theoid-type teeth in some Cunoniaceae (Fig. 15) permitted us to form a secondary outgroup lying outside of the Rosidae. Theoid teeth are found in at least two clades, the thealean clade and the flacourtialean clade (Hickey & Wolfe, 1975), and at this time it is neither clear that the origin of this tooth type is monophyletic nor which of the above clades is more closely related to the Rosidae. Based on this equivocal placement, we chose the Dilleniaceae as our secondary outgroup because of its inferred sister group relationship to the Rosidae, as well as the thealean and flacourtialean clades. The dillenioid tooth type (Figs. 12, 13) is clearly ancestral to the theoid-type tooth (Hickey & Wolfe, 1975) (Figs. 14, 15) and provides an unequivocal secondary outgroup.

A hypothetical ancestor was then formed for polarizing the character states and to root the trees. This was necessary when using PAUP because the program uses one taxon when several outgroups

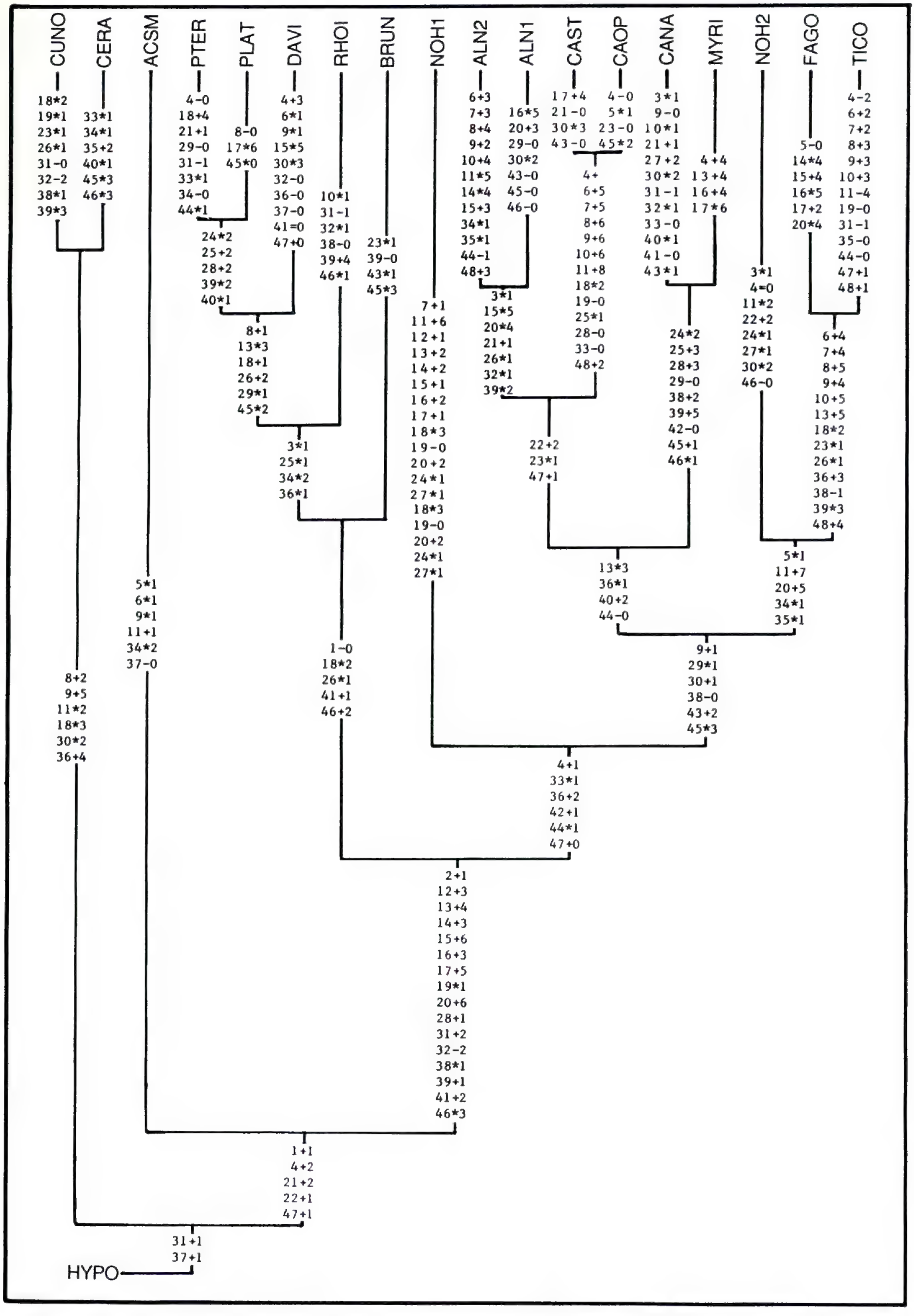
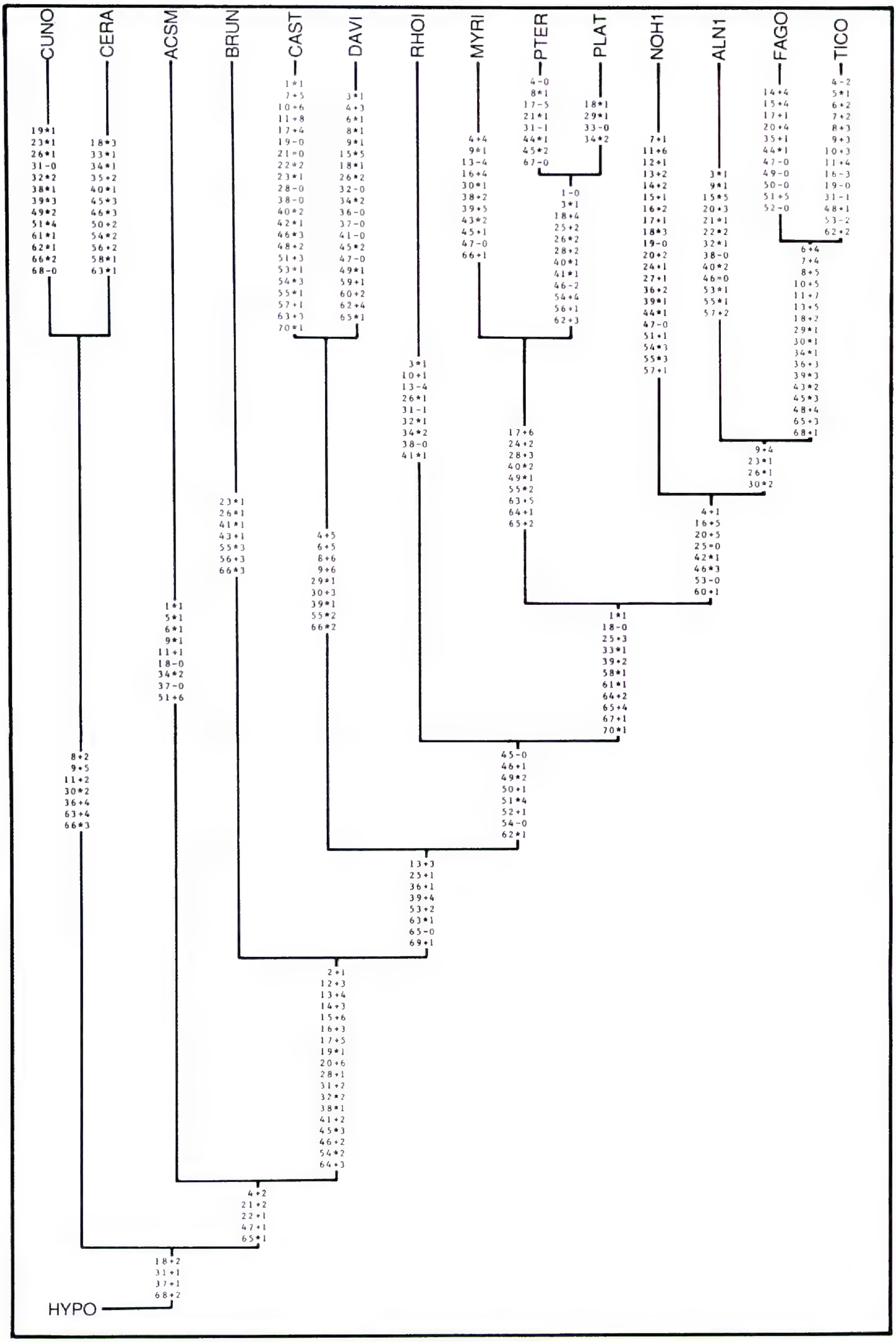


FIGURE 19. Cladogram of data set 1, which includes 48 leaf characters and 18 OTUs (Table 3). This is the shortest tree with 249 steps and a consistency index of 0.550. −, reversal; =, multiple reversal; *, synapomorphy; +, parallelism.


CUNO
19*1
23*1
26*1
31-0
32*2
38*1
39*3
49*2
51*4
61*1
62*1
66*2
68-0
CERA
18*3
33*1
34*1
35*2
40*1
45*3
46*3
50*2
54*2
56*2
58*1
63*1
ACSM
1*1
5*1
6*1
9*1
11*1
18-0
34*2
37-0
51*6
8*2
9*5
11*2
30*2
36*4
63*4
66*3
BRUN
23*1
26*1
41*1
43*1
55*3
56*3
66*3
CAST
1*1
7*5
10*6
11*8
17*4
19-0
21-0
22*2
23*1
28-0
38-0
40*2
42*1
46*3
48*2
51*3
53*1
54*3
55*1
57*1
63*3
70*1
DAVI
3*1
4*3
6*1
8*1
9*1
15*5
18*1
26*2
32-0
34*2
36-0
37-0
41-0
45*2
47-0
49*1
59*1
60*2
62*4
65*1
4*5
6*5
8*6
9*6
29*1
30*3
39*1
55*2
66*2
RHOI
3*1
10*1
13-4
26*1
31-1
32*1
34*2
38-0
41*1
MYRI
4*4
9*1
13-4
16*4
30*1
38*2
39*5
43*2
45*1
47-0
66*1
PTER
4-0
8*1
17-5
21*1
31-1
44*1
45*2
67-0
PLAT
18*1
29*1
33-0
34*2
1-0
3*1
18*4
25*2
26*2
28*2
40*1
41*1
46-2
54*4
56*1
62*3
17*6
24*2
28*3
40*2
49*1
55*2
63*5
64*1
65*2
NOH1
7*1
11*6
12*1
13*2
14*2
15*1
16*2
17*1
18*3
19-0
20*2
24*1
27*1
36*2
39*1
44*1
47-0
51*1
54*3
55*3
57*1
4*1
16*5
20*5
25-0
42*1
46*3
53-0
60*1
ALN1
3*1
9*1
15*5
20*3
21*1
22*2
32*1
38-0
40*2
46-0
53*1
55*1
57*2
9*4
23*1
26*1
30*2
1*1
18-0
25*3
33*1
39*2
58*1
61*1
64*2
65*4
67*1
70*1
45-0
46*1
49*2
50*1
51*4
52*1
54-0
62*1
13*3
25*1
36*1
39*4
53*2
63*1
65-0
69*1
FAGO
14*4
15*4
17*1
20*4
35*1
44*1
47-0
49-0
50-0
51*5
52-0
6*4
7*4
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18*2
29*1
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34*1
36*3
39*3
43*2
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48*4
65*3
68*1
TICO
4-2
5*1
6*2
7*2
8*3
9*3
10*3
11*4
16-3
19-0
31-1
48*1
53-2
62*2
2*1
12*3
13*4
14*3
15*6
16*3
17*5
19*1
20*6
28*1
31*2
32*2
38*1
41*2
45*3
46*2
54*2
64*3
4*2
21*2
22*1
47*1
65*1
18*2
31*1
37*1
68*2
HYPO

are specified. Also, since there is no cladistic analysis of Cunoniaceae, the hypothetical ancestor had to be determined from the most common character states found in the three OTUs of Cunoniaceae. If states were equally common, the state shared with or found in the secondary outgroup was used. Some character states were ordered (see the Appendix). Those characters with only two states were ordered because we were able to specify by outgroup comparison which states were ancestral and which were derived. However, we polarized only a few characters with multiple states, based on structural transformations (see discussion of specific characters in the Appendix). All of our character polarizations are explicit hypotheses of the ancestral character states as well as the structural transformation in the characters that are ordered.

We performed a cladistic analysis as part of our pattern sequence analysis in order to identify the optimal branching pattern. PAUP uses parsimony to find trees with the minimum number of steps. Such an analysis gives hypotheses as to which structural homologies are evolutionarily homologous and which are evolutionarily homoplasous. In addition, it identifies the shared derived characters for each of the clades and taxa. Our analyses included two data sets, one with 48 leaf characters and 18 OTUs (Table 2) and a second that included 70 characters and 14 OTUs (Table 3). The latter data set was subdivided and resulted in three subsets: the first group has all the characters (designated as 2a), the second group (2b) has characters 1 to 48 (the same characters as data set 1) and the third (2c) has characters 49 through 70. Each analysis is summarized in Table 5 and discussed separately below.

The use of global branch swapping for data set 1 resulted in a single shortest tree (Fig. 19) of 249 steps and a consistency index of 0.550 (Table 5). The general topology of this tree has the cunonioid taxa *Ceratopetalum*, *Cunonia*, and *Acsmithia* at the base and a monophyletic origin for the remaining taxa, which are split into two clades. One clade includes the two juglandaceous taxa *Pterocarya* and *Platycarya*, and the OTUs *Davidsonia* and *Brunellia*. The second clade is essentially a fagalean clade with the addition of *Myrica* and *Canacomyrica* (Myricaceae). In this tree, *Ticodendron* is the sister OTU to the fossil genus *Fagopsis*. The set of trees one step longer (Table 5) is similar to the shortest trees in their stability and variability of the topology. Thus it is significant that throughout both sets of trees, the relationships of the taxa of the Cunoniaceae never change, with *Acsmithia* remaining the sister group to the remaining taxa. In addition, these trees always had two clades, though in some trees *Brunellia* was placed as the sister OTU to both clades. Lastly, *Ticodendron* remained well-embedded in the fagoid clade but as a sister OTU to *Castanea* and *Castanopsis* or to *Fagopsis* and *Alnus*2.

We have separated the synapomorphies into four categories based on the characters in our matrices and their distribution on the trees. The first are unistate synapomorphies, in which only one state exists in the entire clade above the node. The next are asymmetrical bistate synapomorphies, in which two states exist above the node, but one is considerably more common than the other. The third are asymmetrical tristate synapomorphies, which have three states above the node, with one much more common. The last are polystate synapomorphies, which have more than three states above the node or have additional states that are nearly as common.

Monophyly of the non-Cunoniaceae taxa is supported by 16 character states. Seven of these characters relate to the origin of what we term the type 2 (rosid) tooth but this tooth type is found in Cunoniaceae and other Rosidae, and it is not clear if its origin is monophyletic. Most of the synapomorphies for the clade are polystate. The exceptions include alternate leaf arrangement (character 2), which is a unistate synapomorphy; medial position of the principal vein in a type 2 tooth (12), an asymmetrical bistate synapomorphy; and stipule base that is wider than its attachment to the axis (28)—an asymmetrical tristate synapomorphy. The juglandoid clade is supported by six character states of which two are asymmetrical bistate synapomorphies. These are branching of the secondary veins common (46) and slightly zig-zag branching of the twigs (41). The fagoid clade is supported by six character states and all of the synapomorphies are polystate.

The analysis of data set 2a using global branch

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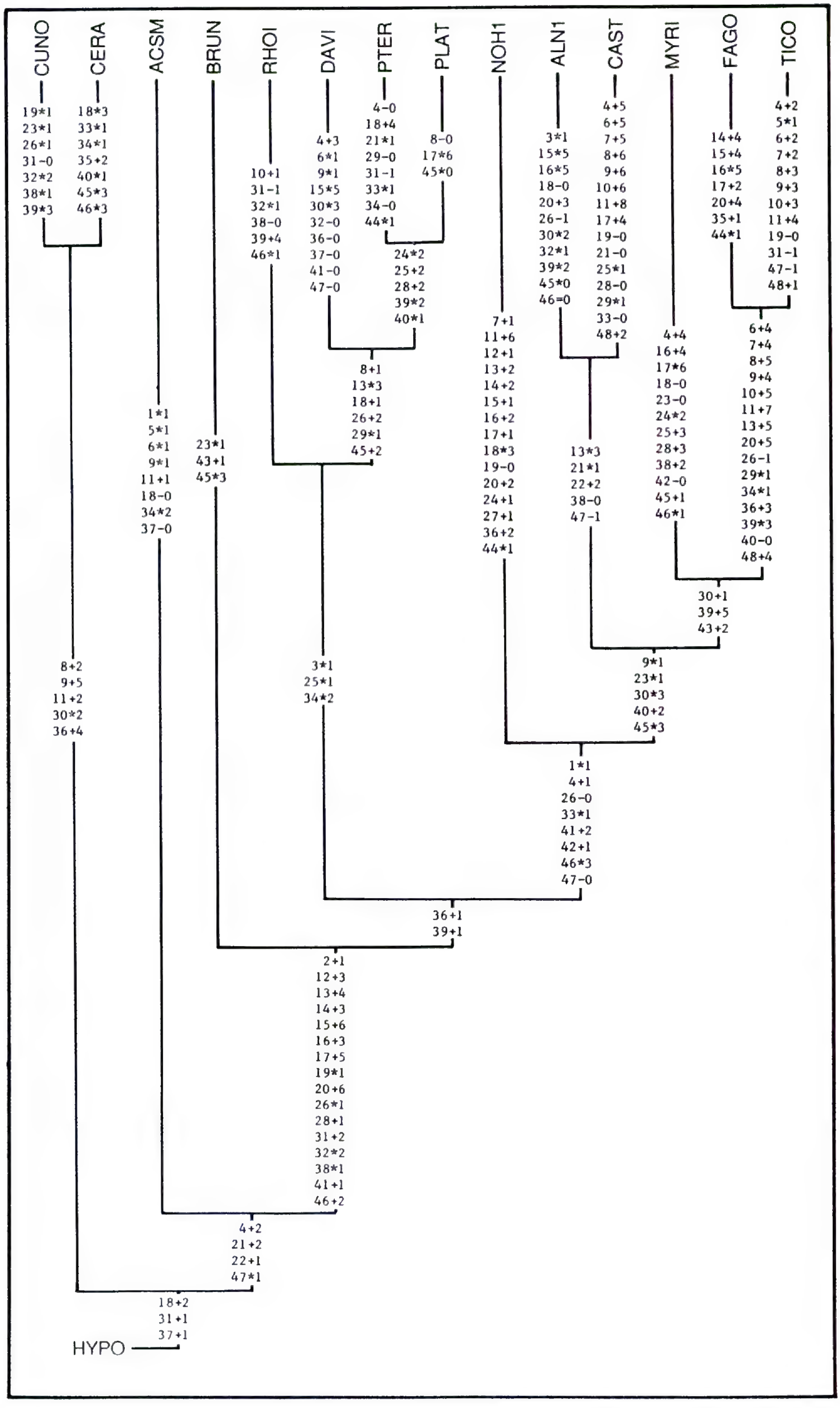
FIGURE 20. Cladogram of data set 2a, which includes 70 vegetative and reproductive characters and 14 OTUs. This is one of the two shortest trees with 294 steps and a consistency index of 0.609. The other shortest tree differs only by having *Davidsonia* as the sister OTU to all the higher taxa including *Castanea*, and *Castanea* becomes the sister taxon to the remaining OTUs. −, reversal; =, multiple reversal; *, synapomorphy; +, parallelism.


CUNO
19*1
23*1
26*1
31-0
32*2
38*1
39*3
CERA
18*3
33*1
34*1
35+2
40*1
45*3
46*3
8+2
9+5
11+2
30*2
36+4
ACSM
1*1
5*1
6*1
9*1
11+1
18-0
34*2
37-0
BRUN
23*1
43+1
45*3
RHOI
10+1
31-1
32*1
38-0
39+4
46*1
8+1
13*3
18+1
26+2
29*1
45+2
3*1
25*1
34*2
DAVI
4+3
6*1
9*1
15*5
30*3
32-0
36-0
37-0
41-0
47-0
PTER
4-0
18+4
21*1
29-0
31-1
33*1
34-0
44*1
PLAT
8-0
17*6
45*0
24*2
25+2
28+2
39*2
40*1
NOH1
7+1
11+6
12+1
13+2
14+2
15+1
16+2
17+1
18*3
19-0
20+2
24+1
27+1
36+2
44*1
ALN1
3*1
15*5
16*5
18-0
20+3
26-1
30*2
32*1
39*2
45*0
46=0
13*3
21*1
22+2
38-0
47-1
CAST
4+5
6+5
7+5
8+6
9+6
10+6
11+8
17+4
19-0
21-0
25*1
28-0
29*1
33-0
48+2
9*1
23*1
30*3
40+2
45*3
1*1
4+1
26-0
33*1
41+2
42+1
46*3
47-0
MYRI
4+4
16+4
17*6
18-0
23-0
24*2
25+3
28+3
38+2
42-0
45+1
46*1
30+1
39+5
43+2
FAGO
14+4
15+4
16*5
17+2
20+4
35+1
44*1
6+4
7+4
8+5
9+4
10+5
11+7
13+5
20+5
26-1
29*1
34*1
36+3
39*3
40-0
48+4
TICO
4+2
5*1
6+2
7+2
8+3
9+3
10+3
11+4
19-0
31-1
47-1
48+1
36+1
39+1
2+1
12+3
13+4
14+3
15+6
16+3
17+5
19*1
20+6
26*1
28+1
31+2
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22+1
47*1
18+2
31+1
37+1
HYPO

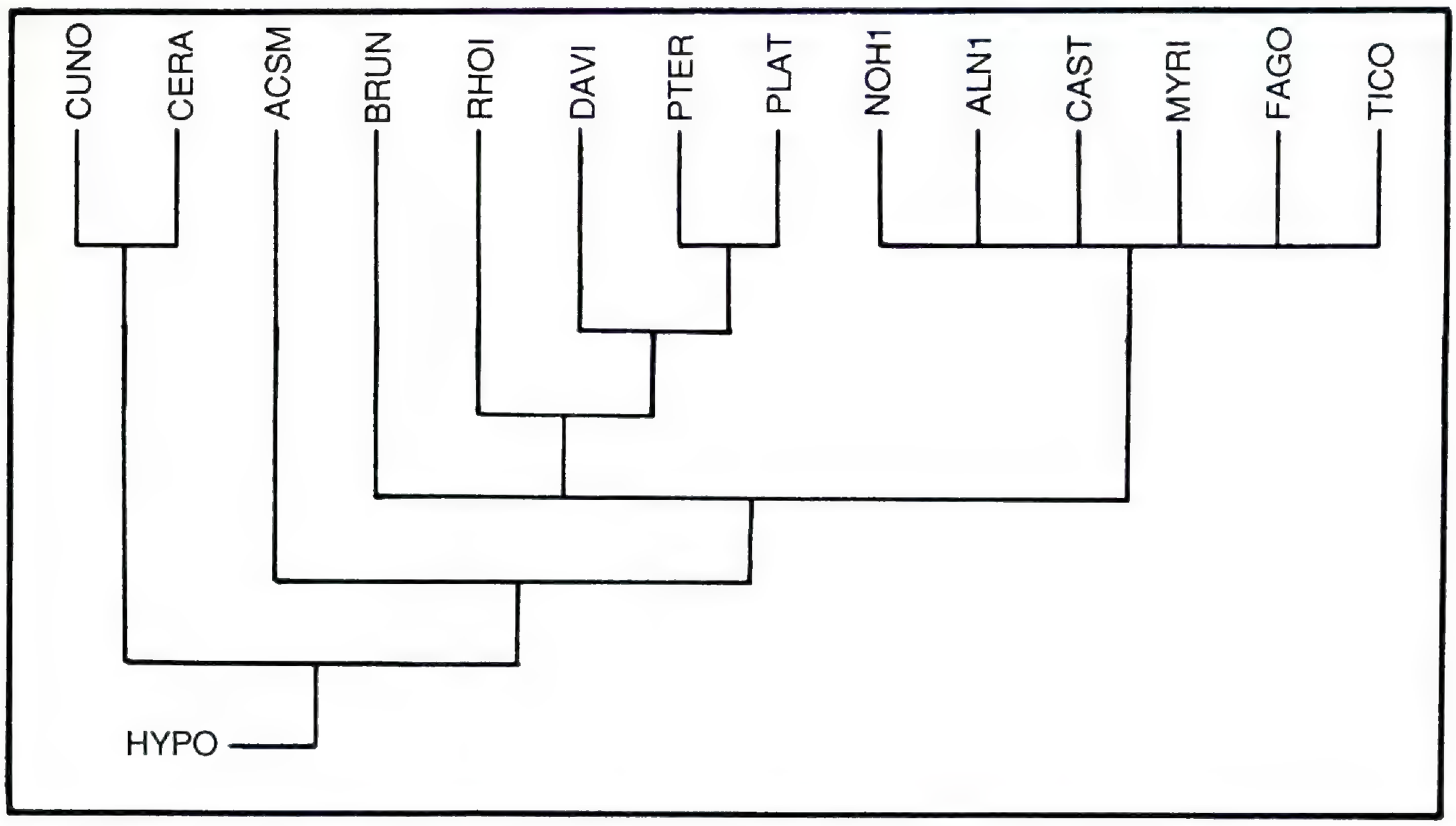

FIGURE 22. Strict consensus tree of the nine trees with the shortest length from data set 2b.

swapping (Fig. 20) resulted in two trees with 294 steps and a consistency index of 0.609 (Table 5). The general layout of the trees has the cunonioid taxa at the base and the remaining taxa forming a monophyletic group derived from *Acsmithia*. The other Rosales, *Brunellia* and *Davidsonia*, are at the base of this clade, followed by *Rhoiptelea* and the remaining hamamelid taxa, except that *Castanea* is placed as a sister group to *Davidsonia*. Again, *Ticodendron* is well-embedded at the top of the hamamelid clade near members of Fagales as a sister OTU to *Fagopsis*. This topology remains quite consistent in the other most parsimonious trees, with the only difference being that instead of having *Davidsonia* and *Castanea* as sister taxa, *Davidsonia* becomes the sister OTU to all the higher taxa including *Castanea*, which in turn becomes the sister taxon to the remaining members. The next most parsimonious tree, with one additional step, also has the same topology.

The monophyly of the taxa derived from the cunonioid *Acsmithia* is supported by 18 character states. Again, seven refer to character states of the rosid (type 2) tooth. A unistate synapomorphy is alternate leaf arrangement (character 2), while the medial position of the principal vein (12) in a rosid tooth is a bistate synapomorphy. The presence of both admedial and accessory veins (14) is a tristate synapomorphy. Relationship of *Ticodendron* to the upper hamamelid clade is given by eight character states. A fused bract-bracteole complex (60) is a unistate synapomorphy, while an acuminate/acuminate (4) tooth shape is a bistate synapomorphy.

The cladistic analysis of data set 2b, performed with global branch swapping (Fig. 21), resulted in nine trees with a length of 204 steps and a consistency index of 0.627 (Table 5). The general topology of the tree has the OTUs of the Cunoniaceae at the base, and the remaining taxa forming a monophyletic group derived from *Acsmithia*. *Brunellia* appears next as a sister OTU to the remaining taxa that are again divided into two clades. One is the juglandoid clade with *Pterocarya*, *Platycarya*, and *Rhoiptelea*, while the second is the fagoid clade with the remaining taxa. *Ticodendron* is well-embedded in the fagoid clade and is the sister OTU to *Fagopsis*. A strict consensus tree of all nine most parsimonious trees (Fig. 22) shows the major differences from the tree described above (Fig. 21). Here the upper hamamelid clade is unresolved, as are the three clades leading to

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FIGURE 21. Cladogram of data set 2b, which includes 48 leaf characters and 14 OTUs. This is one of the nine shortest trees (consensus tree in Fig. 22) with 204 steps and a consistency index of 0.627. −, reversal; =, multiple reversal; *, synapomorphy; +, parallelism.

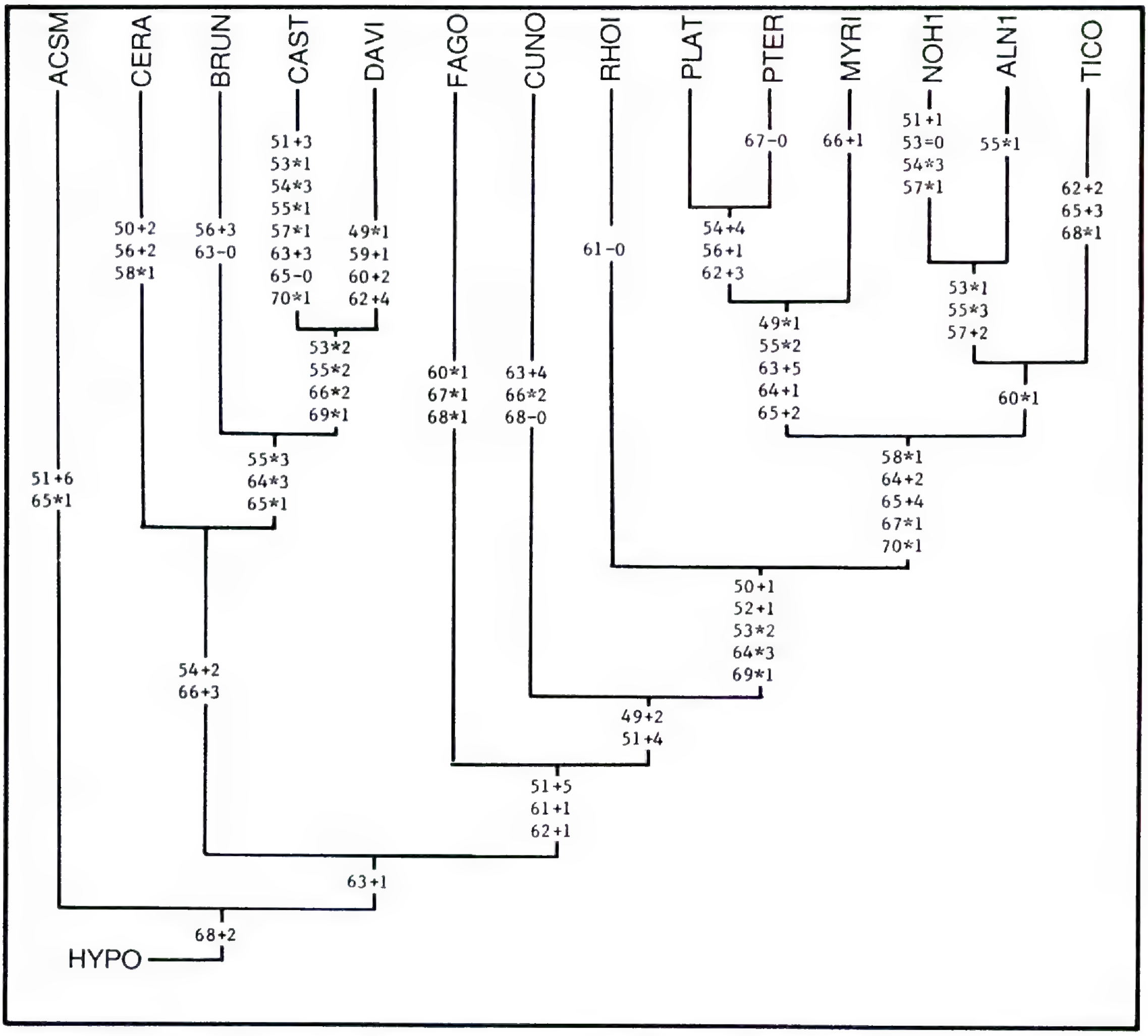

FIGURE 23. Cladogram of data set 2c, which includes 22 reproductive and wood characters and 14 OTUs. This is one of the three shortest trees (consensus tree in Fig. 24) with 74 steps and a consistency index of 0.689. −, reversal; =, multiple reversal; *, synapomorphy; +, parallelism.

Brunellia, the Juglandaceae, and the upper hamamelids.

In data set 2b, the monophyly of the taxa derived from *Acsmithia* is supported by 16 character states of which seven refer to character states of the type 2 (rosid) tooth. The only unistate synapomorphy is alternate leaf arrangement (character 2), while the medial position of the principal vein (12) in a type 2 (rosid) tooth is a bistate synapomorphy. The presence of both admedial and accessory veins (14) is a tristate synapomorphy. The juglandoid clade is supported by three states while the fagoid clade is supported by eight states. The latter has one unistate synapomorphy—zig-zag twig branching (41)—and one bistate synapomorphy—axillary buds out of the plane of the leaf (42).

Our analysis of data set 2c, again using global branch swapping, produced three trees (Fig. 23) that had a length of 74 steps and a consistency index of 0.689 (Table 5). The general topology has *Acsmithia* at the base with the remaining taxa forming a monophyletic group. This is split in turn into two groups, the first with *Davidsonia*, *Castanea*, *Brunellia*, and *Ceratopetalum*, and the second with the remaining taxa. Note that the second clade includes *Cunonia* (Cunoniaceae). *Ticodendron* is well-embedded in the second clade near some of the fagalean taxa. There are two other equally parsimonious trees. The only variation from this pattern is the relationships among *Ticodendron*, *Alnus*1, and *Nothofagus*1 as shown in the strict consensus tree (Fig. 24).

In this tree (Fig. 23) the monophyly of the taxa derived from *Acsmithia* is supported by a single polystate synapomorphy. The *Ceratopetalum*/*Brunellia* clade is supported by one bistate synapo-

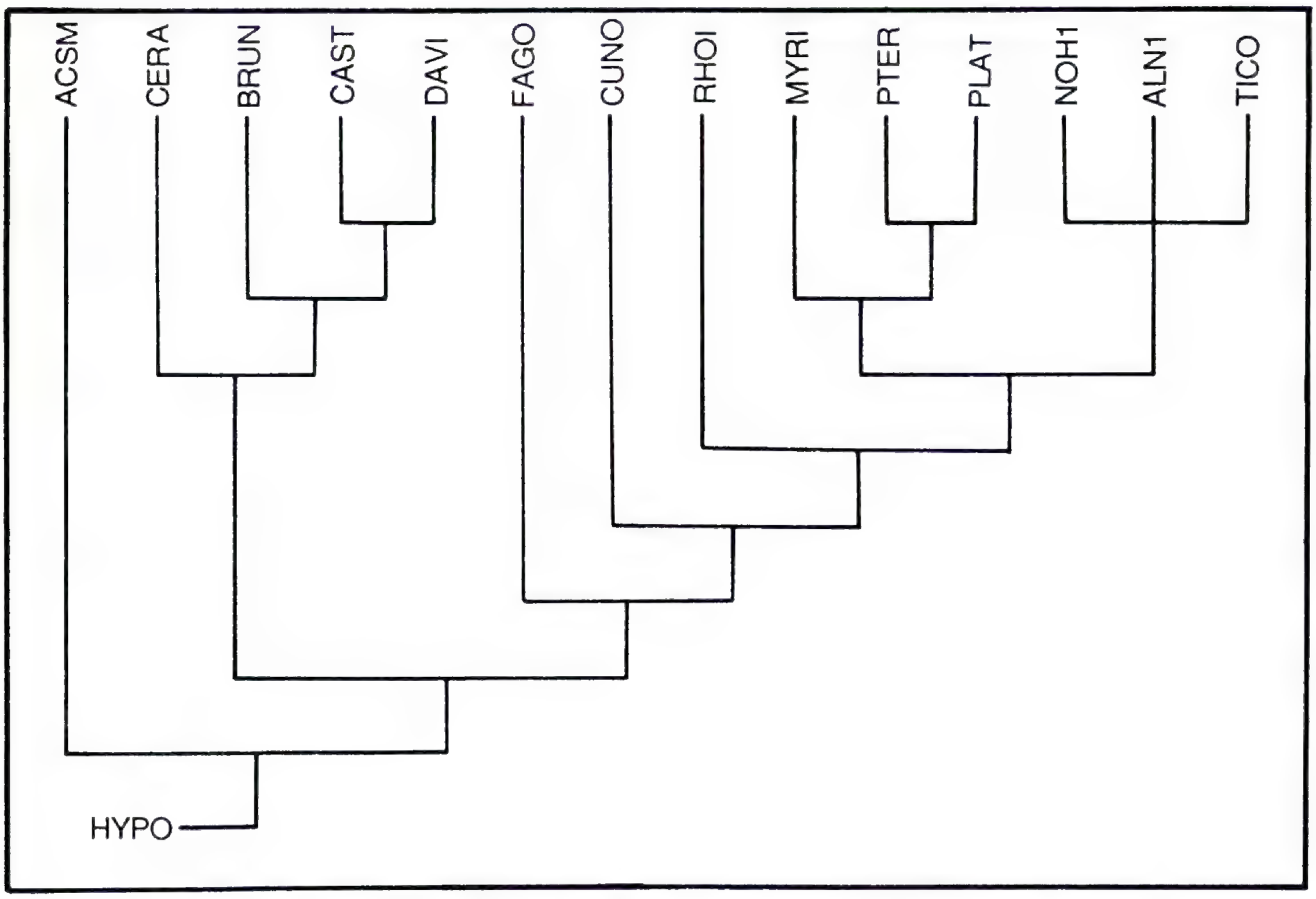

FIGURE 24. Strict consensus tree of the three trees with the shortest length from data set 2c.

morphy—vessels whose perforation plates are simple or scalariform with only a few bars (54). The second clade includes the remaining taxa and is supported by three characters of which two are unistate synapomorphies. These states include verrucate pollen sculpturing (51) and a simple, unbranched inflorescence (61).

In addition to these data sets we tried several experimental sets (Table 6). In these trials we attempted to use partially a priori methods to reduce the number of characters that were inappropriate for this hierarchy. We did this in order to resolve the situation that arises as the scope of a phylogenetic analysis is broadened to include more divergent groups, which causes certain characters to become homoplasous. Thus, in any randomly chosen set of characters, some characters will be more appropriate for comparisons at low hierarchical levels and some at higher. We thus devised a filtering method that was based on our two outgroups, Cunoniaceae and Dilleniaceae, to select characters appropriate to the hierarchy we examined. We suggest that if there is variability of characters between outgroups it may indicate a potentially homoplasous character for the ingroup. Our method was simply to remove any character that did not have any states shared in both outgroups.

In this way, 26 characters were removed, 25 from the leaf character set (1–48) and 1 from the list of other characters (49–70; Table 6). Although the topologies subsequently derived using these sets are generally similar to those found in the previous analyses, the cunonioid taxa switched position, with *Acsmithia* at the base and *Ceratopetalum* and *Cunonia* as sister taxa that together form the sister group to the remaining taxa. This is a particularly interesting result in light of previous suggestions that *Acsmithia* may be the most primitive genus in the Cunoniaceae (Dickison, 1989). The resulting tree lengths and consistency indexes are shown in Table 6. As one would expect, a smaller character base decreased the tree lengths and increased the consistency index; however, the resolution decreased because there were more trees of the same length. Note that, although the leaf data set (2b) had nearly the same number of characters as the nonleaf set (2c), the consistency index of the former was considerably higher. This suggests that these leaf characters may be better for resolving these relationships at the familial level among the so-called Amentiferae than the combination of reproductive and wood characters making up set 2c.

The sum of our cladistic analyses shows several general and recurrent similarities. *Ticodendron* is consistently placed with members of the Fagales

TABLE 6. Experimental data sets with characters removed. The characters in parentheses are the number of characters. The major options are addition of sequence = closest (closest), addition of sequence = simple (simple), unordered in part (part), and unordered all (all). Data set 1 included characters 1–48 and 18 OTUs, and data set 2 included all or parts of characters 1–70 and 14 OTUs.

Data set options	Number of trees	Length of trees	Consistency index
Data set 1 (23)			
Closest part	47	110	0.682
Simple part	47	110	0.682
Closest all	47	110	0.682
Simple all	47	110	0.682
Data set 2			
a All characters (54)			
Closest part	8	177	0.667
Simple part	8	177	0.667
Closest all	8	176	0.670
Simple all	8	176	0.670
b Characters 1–48 (23)			
Closest part	10	94	0.745
Simple part	10	94	0.745
Closest all	10	94	0.745
Simple all	10	94	0.745
c Characters 49–70 (21)			
Closest part	18	70	0.686
Simple part	18	70	0.686
Closest all	18	70	0.686
Simple all	18	70	0.686

and occasionally Myricaceae. The base of the clade is always found to lie with members of Cunoniaceae and other taxa considered to be members of the Rosidae by Takhtajan (1969, 1980) and Cronquist (1981, 1988). From our analyses it appears that Cunoniaceae may not be a monophyletic group, but we have not sampled the family sufficiently to show this. A major exception to the consistency of our analyses is the placement of *Fagopsis*, which switched from the top of the tree to near *Cunonia* near the base in data set 2c. This variability is probably due to the number of unknown character states in this fossil taxon.

Examination of the similarity matrices also shows comparable results (Table 4). *Ticodendron* is most similar to Fagales in data sets 1 and 2b, based on leaf data, though it is also similar to *Brunellia* and *Rhoiptelea*. The nonleaf data set (2c) also shows *Ticodendron* to be similar to Fagales and *Myrica* but with strong similarities as well to the two juglandaceous taxa and *Rhoiptelea*. Overall, *Ticodendron* is similar to the two fagalean taxa *Fagopsis* (0.491) and *Alnus*1 (0.478), as well as to *Rhoiptelea* (0.471), *Myrica* (0.429), *Nothofagus*1 (0.426), and *Platycarya* (0.400) when all characters are included, as in data set 2a of Table 4.

Both the similarity matrices and the cladistic analyses show that the leaf and the nonleaf data sets have higher internal similarities or consistencies than does the combined data set. We suggest that this is partly due to the lack of evolutionary homology in some of the characters. In particular, the Normapolles-type pollen that is found in many members of Hamamelidae (e.g., *Pterocarya*, *Platycarya*, *Rhoiptelea*, *Myrica*, *Alnus*, and *Ticodendron*) and thought to be a natural group marked by synapomorphies (Muller, 1984), may actually have evolved more than once (Batten & Christopher, 1981; Batten, 1986; Kedves, 1989). Thus the pollen characters of this group may act to force these taxa together artificially. Another suite of characters that may have evolved independently is that of reduced flowers. Since reduced flowers of similar morphology are found in other nonrosid hamamelids (e.g., Urticales; Thorne, 1989), these are probably homoplasous characters.

Similarly, some leaf characters may be evolutionarily homoplasous at this familial level of analysis. These suspicions were confirmed when we ran experimental data sets in which about half of the characters were dropped, resulting in a dramatic increase in the consistency index. The fact that some of our leaf characters are evolutionarily homoplasous is not surprising at this early stage in the development of leaf architectural methods. As future studies refine the use of these characters our knowledge of their variability at various taxonomic levels will be established.

CONCLUSIONS

Based on these analyses we suggest the following relationships. *Ticodendron* is most similar to an extinct taxon of Oligocene age known as *Fagopsis* (Manchester & Crane, 1983), and both of these taxa are most similar to members of the families Fagaceae and Betulaceae (in the sense of Cronquist, 1981). Manchester & Crane (1983) placed *Fagopsis* in the Fagaceae, but we do not feel that the structure of the female inflorescence or details of leaf architecture support assignment to that family. *Rhoiptelea* is a centrally placed taxon with relationships to both the juglandoid clade and the fagoid clade. *Davidsonia* is probably a sister taxon to Juglandaceae. Cunoniaceae is the sister group to all these taxa and has characters that are transitional to members of Dilleniidae as well. The

Cunoniaceae also appear to be paraphyletic but this needs further study.

From the standpoint of its systematic placement, therefore, our analysis demonstrates that the affinities of *Ticodendron* lie with the order Fagales (sensu Cronquist, 1981) but that it is clearly distinct from any of the families that are currently understood as belonging there. We therefore recommend that *Ticodendron* be recognized as a separate monotypic family of the Fagales. Although clearly closely related, the status of the fossil genus *Fagopsis* in relation to the new family is unclear because of a number of missing characters as well as the rather specialized nature of the fruiting structures in *Fagopsis*.

In addition to indicating the relationships of *Ticodendron*, this study demonstrates the utility of leaf characteristics. Comparisons of the consistency index of data sets 2b (leaf) and 2c (nonleaf) show very little difference. This indicates that these characteristics are as useful as floral, pollen morphological, and most anatomical characters that have traditionally been used in plant systematics. Interestingly, when we attempted to filter inappropriate characters from the experimental sets, we found that the consistency index of the leaf data set dramatically improved (Table 6). The leaf set had 23 characters and a consistency index of 0.745 while the nonleaf set had 21 characters and a consistency index of 0.686.

We believe that the best approach to such analyses is to select characteristics based on their information content at the appropriate hierarchical level. Our experimental data suggest that, for this level of the taxonomic hierarchy, the leaf data set probably includes more congruent characters than the set that includes characters from the highly reduced, largely wind-pollinated inflorescences of the Amentiferae (Thorne, 1989). Thus the leaf data set may actually be superior to the nonleaf set at this hierarchical level in this group of plants.

Finally, we feel that the analysis presented here has provided a plausible and consistent resolution for the surprisingly difficult systematic problems presented by this unusual new taxon. We also hope that this effort has shed some new light on the evolution of that group of rosid/hamamelid taxa loosely known as the Amentiferae and has elucidated some of the methods and characters whereby that analysis could be extended still further.

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APPENDIX. Characters and character states for the data matrices (Tables 2, 3) used to produce the cladograms in Figures 19–24, discussion of characters, and data on taxa that had more than one character state for each. The ancestral state based on outgroup comparison is 0; * indicates that the character states are ordered; NA indicates not applicable.

1. *Leaf organization: 0 pinnate compound, 1 simple.

True pinnate leaves, as opposed to ternately compound leaves, first appear in Rosales. Yet, in the primitive families, such as Brunelliaceae and Cunoniaceae, the leaf organization is not canalized, with both types found in the same genus and sometimes species. All leaves could be clearly assigned to one of the character states except for *Davidsonia*. This species is assigned the pinnately compound state, even though it is actually pinnatisect, with wings between the pinnae on the leaf axis.

2. *Leaf arrangement: 0 opposite, 1 alternate.

Opposite leaves are not common in this group of OTUs nor in the primitive Dilleniidae or Rosidae. *Nothofagus* has a few species that are opposite.

Leaf margin:

3. *Margin: 0 toothed in one order, 1 toothed in more than one order.

This character refers to a situation where there is a second order of teeth originating on the margins of the first. Two orders of teeth are widely distributed but not found in closely related clades.

4. Tooth shape (apical and basal margins): 0 concave, convex, 1 convex, convex, 2 concave, concave, 3 concave, acuminate, 4 acuminate, acuminate, 5 concave, straight.

The first term refers to the apical side and the second to the basal side of the tooth. There is considerable variation in tooth shape, which is dependent on basic tooth type, and specific derived modification of the types. *Canacomyrica* had both character state 1 and teeth that are convex, acuminate. In *Alnus* the small teeth are concave, concave.

5. *Sinus shape: 0 angular, 1 smooth.

Angular sinuses are the most common type in angiosperms and in this group. *Castanea* and *Castanopsis* have both character states.

Tooth type 1: this type has the principal vein originating from close to the sinus and has no accessory vein along the admedial side.

This basic tooth type has previously been called cunonioid (Hickey & Wolfe, 1975) and our recent studies show that it is similar to the third tooth found in the

primitive Dilleniidae. All the ancestral character states are found in theoid teeth.

6. Position of principal vein of tooth type 1: 0 lateral toward apical sinus, 1 medial, 2 *Ticodendron* NA, 3 Betulaceae NA, 4 *Fagopsis* NA, 5 Fagaceae NA.

Platycarya most commonly medial (1) but also lateral (0).

7. Course of principal vein of tooth type 1: 0 apically deflected, 1 nothofagoid, principal displaced to sinus, 2 *Ticodendron* NA, 3 Betulaceae NA, 4 *Fagopsis* NA, 5 Fagaceae NA.

Some *Brunellia* are slightly basally deflected; *Acsmithia* are usually straight and only sometimes 0.

8. The presence of veins associated with the principal vein of tooth type 1: 0 both admedial and accessory, 1 only admedial, 2 only accessory, 3 *Ticodendron* NA, 4 Betulaceae NA, 5 *Fagopsis* NA, 6 Fagaceae NA.

In *Platycarya* the veins are usually missing and only sometimes are accessories found (2).

9. Strength of admedial vein of tooth type 1: 0 same vein order, 1 lower vein order, 2 Betulaceae NA, 3 *Ticodendron* NA, 4 *Fagopsis* NA, 5 Cunoniaceae NA, 6 Fagaceae NA.

10. Course of conjunctal veins close to tooth apex of tooth type 1: 0 none, 1 single, 2 in alternate pairs, 3 *Ticodendron* NA, 4 Betulaceae NA, 5 *Fagopsis* NA, 6 Fagaceae NA.

Rhoiptelea may be either none (0) or single (1).

11. Major vein(s) closest to sinus of tooth type 1: 0 admedial, 1 accessory or branch, 2 principal, 3 admedial and accessory, 4 *Ticodendron* NA, 5 Betulaceae NA, 6 nothofagoid: branch from principal, 7 *Fagopsis* NA, 8 Fagaceae NA.

Tooth type 2: this type has the principal vein originating medially and has at least a few teeth with an accessory vein along the admedial side.

The transitions between teeth in taxa with both types of teeth, transitions between taxa with only one type of tooth, and outgroup comparison suggest that type 2 teeth are derived from type 1. Note that in leaves with both types, type 2 teeth are associated with strong secondaries.

12. Position of principal vein of tooth type 2: 0 Cunoniaceae NA, 1 *Nothofagus* NA, 2 Brunelliaceae NA, 3 medial.

Although the teeth of the Magnoliidae and Dilleniaceae are medial, so are some type 1 teeth and theoid teeth.

13. Course of principal vein of tooth type 2: 0 Cunoniaceae NA, 1 Brunelliaceae NA, 2 *Nothofagus* NA, 3 straight, 4 apically deflected, 5 basally deflected.

The principal vein in *Fagopsis* is mostly straight (3) but occasionally basally deflected (5), and in *Platycarya* mostly straight (3) and sometimes apically deflected (4).

14. Presence of veins associated with principal vein of tooth type 2: 0 Cunoniaceae NA, 1 Brunelliaceae NA, 2 *Nothofagus* NA, 3 both admedial and accessory, 4 only accessory.

15. Strength of admedial vein of tooth type 2: 0 Cunoniaceae NA, 1 *Nothofagus* NA, 2 Brunelliaceae NA, 3 Betulaceae NA, 4 *Fagopsis* NA, 5 lower vein order, 6 same vein order.

16. Course of conjunctal veins of tooth type 2: 0 Cunoniaceae NA, 1 Brunelliaceae NA, 2 *Nothofagus* NA, 3 in opposite pairs, 4 in alternate pairs, 5 none.

Ticodendron mostly has only an admedial, but when there are conjunctals, they are in opposite pairs (3). *Myrica* has mostly alternate conjunctals (4) but occasionally opposite (3).

17. Fusion of principal and conjunctal veins of tooth type 2: 0 Cunoniaceae NA, 1 *Nothofagus* NA, 2 *Fagopsis* NA, 3 Brunelliaceae NA, 4 Fagaceae NA, 5 separate, 6 fused.

18. Termination of medial vein at apex of tooth: 0 splayed, 1 attenuate, 2 tapered, 3 truncated, 4 bulbous.

Nothofagus (2) has both splayed and bulbous terminations. *Brunellia* may be splayed (0) or tapered (2), *Canacomyrica* is tapered (2) but sometimes truncated (3), and *Myrica* is usually truncated (3) and less commonly splayed (0).

19. *Sinus bracing of teeth: 0 not braced, 1 braced by convergent thickened veins.

Not braced (0) is the state found in most teeth of angiosperm leaves. *Brunellia* may be not braced (0) or braced (1).

20. Major vein(s) closest to sinus of tooth type 2: 0 Cunoniaceae NA, 1 Brunelliaceae NA, 2 *Nothofagus* NA, 3 admedial, 4 accessory or branch, 5 conjunctal or branch, 6 admedial and accessory.

Nothofagus usually has a branch from the admedial and rarely just the admedial (3).

21. Glandularity of tooth apex: 0 glandular, dark, 1 glandular, translucent, 2 nonglandular.

Glandular, dark apices (0) are found in the theoid tooth type; presumably homoplasous clear, glandular terminations are found in ancestral forms such as the Dilleniales. *Castanopsis* usually has character state 2 but occasionally has character state 0.

22. Apical morphology of teeth in cleared leaf preparations of mature leaves: 0 setaceous, 1 simple, 2 tylate.

Setaceous apices occur in theoid teeth and in presumed evolutionary transitions to that type.

Castanopsis is usually simple but sometimes tylate.

23. *Characteristics of the leaf base or petiole: 0 does not encircle the axis, stipules discrete or missing, 1 encircles the axis (> 50% at apical nodes or if opposite, > 40%) and forms sheath or stipules.

Discrete stipules on the main axis apparently first appear in Rosales and the primitive, palmate Dilleniidae.

24. Presence of wings on the petiole or stipules associated with the base of the petiole: 0 has stipules, 1 has both wings and stipules, 2 no wings or stipules.

Wings are stipules associated with encircling leaf bases and are common in the Magnoliidae and primitive Dilleniidae.

25. Stipules deciduous below the second node with ex-

panded leaves: 0 yes, always deciduous, 1 no, not usually deciduous, 2 Juglandaceae NA, 3 Myricaceae NA.

Stipules generally appear deciduous in primitive groups. *Castanopsis* and *Castanea* both may have twigs that are deciduous (0) while others are nondeciduous (1).

26. Petiole attachment: 0 enlarged base without stipules attached, 1 enlarged base with portion of stipule attachment on base, 2 without enlarged base.

The distribution of this character is unclear. *Brunellia* and *Castanea* may be enlarged (1) or not enlarged (2).

27. Petiole scar: 0 3(4) trace/3 lacunar, 1 arc of more than 4 traces, 2 no scars visible.

Castanopsis and *Castanea* both have character states 0 and 1.

28. Stipule base: 0 not wider than attachment, 1 wider than attachment, 2 Juglandaceae NA, 3 Myricaceae NA.

Distribution of this character is unclear but from our observations it appears that stipules with narrow attachments (1) do not appear until the level of Flacourtiaceae and Cunoniaceae.

29. *Principal venation: 0 pinnate semicraspedodromous, 1 craspedodromous.

Semicraspedodromous (0) is the general case in the primitive Dilleniidae and Rosidae. Craspedodromy is rare but found in the isolated clade originating in Dilleniaceae (e.g., *Doliocarpus*) and including Actinidiaceae. However, because of the difference in tooth type in their clade, the craspedodromous state here represents a homoplasy with the craspedodromous veins (1) of the Rosidae. *Davidsonia* usually has character state 1 but occasionally also 0, and *Myrica* is both brochidodromous and semicraspedodromous (0).

30. Angle of origin of lower basal veins: 0 with two pairs at a lower angle and subsequent at a higher angle though may be somewhat irregular in angle and spacing, 1 with basal no different in angle or spacing, 2 with basal pair at a lower angle and subsequent at a higher angle though may be somewht irregular in angle and spacing, 3 basal vein at highest angle with subsequent veins at lower angles, 4 actinodromous.

Distribution of this character is variable, although it appears that those with two pairs at a lower angle (0) are more common in the primitive angiosperms.

31. Areoles: 0 incomplete, 1 imperfect, 2 well developed.

Incomplete areoles (0) are found throughout the primitive angiosperms and those with low-rank leaves.

32. Marginal venation: 0 incomplete, spiked, 1 incompletely looped, 2 looped.

Distribution of this character is unclear.

33. *Number of deuterals: 0 greater than 18, 1 less than or equal to 18.

Distribution of this character is incompletely known, but in primitive angiosperm groups the number of deuterals is usually less than 10.

34. Number of deuterals + opadials: 0 19–28, 1 less than or equal to 18, 2 greater than 28.

Distribution of this character is incompletely known, but in primitive angiosperm groups the number of deuterals is usually less than 10, plus opadials is usually less than 15.

35. Number of deuterals + opadials + trinals: 0 greater than 60, 1 41–60, 2 less than or equal to 40.

Distribution of this character is incompletely known, but in ancestral angiosperm groups the D-O-T number is usually less than 35 in unreduced leaves.

36. Trichome type: 0 simple, 1 glandular/peltate and simple, 2 glandular/peltate, 3 T-shaped, 4 Cunoniaceae NA.

Distribution of this character is unclear.

37. *Stomate type: 0 paracytic, 1 anomocytic, 2 variable.

Both paracytic (0) and anomocytic (1) stomates have a variable distribution in primitive angiosperms.

38. Dehision of tooth tip in young expanding leaf: 0 nondeciduous, 1 deciduous, 2 none.

Nondeciduous tooth apices are the general case among primitive angiosperms.

39. Shape of tooth tip in young expanding leaf: 0 short, stout, 1 elongate, capitate, 2 short, capitate, 3 elongate, simple, 4 *Rhoiptelea* NA, 5 *Myrica* NA.

Distribution of this character is unclear.

40. Direction of apex of tooth tip in young expanding leaf: 0 pointing abaxially, 1 pointing adaxially, 2 in plane of lamina.

Distribution of this character is unclear.

41. Branching of twigs: 0 straight, 1 slightly zig-zag, 2 zig-zag.

Distribution of this character is unclear. *Castanopsis* and *Castanea* are zig-zag (2) to slightly zig-zag (1).

42. *Axillary buds: 0 in plane of leaf base(s), 1 out of plane of leaf base(s).

Axillary buds in plane of leaf base (0) is the expected state for primitive angiosperms, but our observations of this character are incomplete.

43. *Uniformity of course of basal secondaries compared to distal portion of leaf. 0 no, 1 nearly so, 2 yes.

Lack of uniformity in secondaries (0) is the general case in primitive angiosperms. Uniform, or nearly uniform (2, 1) secondaries have a similar distribution to character 29.

44. *Existence of comb vein: 0 present, 1 absent.

Distribution of this character is unclear, although comb veins are often found in craspedodromous leaves.

45. *The existence of intersecondaries: 0 common (greater than 40%), 1 few (3 to 5), 2 rare (1 or 2), 3 none (never any).

Intersecondaries are frequently found in the magnoliids and are lost in numerous groups of more derived dicots.

46. Branching of secondaries: 0 rare (1 or 2), 1 few (3 to 5), 2 common (greater than 40%), 3 none (never any).

Branched secondaries are common among the Magnoliidae.

47. *Base of a number of leaves or terminal leaflets asymmetrical: 0 none (never any), 1 common.

Distribution of this character is unclear.

48. In type 1 teeth: 0 principal vein originates from near sinus, 1 *Ticodendron* NA, 2 Fagaceae NA, 3 Betulaceae NA, 4 *Fagopsis* NA.

49. Pollen shape: 0 prolate, spherical, 1 suboblate, spherical, 2 oblate.

The prolate to spherical shape (0) appears throughout the primitive triaperturate groups.

50. Pollen aperture: 0 colporate, 1 porate, 2 colpate.

The colpate condition appears throughout the primitive triaperturate groups, while the colporate condition (0) does not appear until the level of Flacourtiaceae and Cunoniaceae. The porate condition found in the Normapolles group probably had multiple origins. *Cunonia* is both colporate (0) and colpate (2).

51. Pollen sculpturing and density: 0 reticulate, 1 spinulose, moderate, 2 spinulose, few, 3 striate, 4 spinulose, many, 5 verrucate, 6 psilate/perforate.

Reticulate sculpturing (0) appears throughout the primitive triaperturate groups. *Cunonia* is both reticulate (0) and spinulose, many (4).

52. *Exine type tectate/perforate: 0 columellate, 1 columellate-granular.

Columellae (0) appear throughout primitive angiosperms. The coding of Cunoniaceae is uncertain and needs TEM sections.

53. Exine proportions: 0 sexine greater than or equal to nexine, 1 sexine greater than nexine, 2 sexine much greater than nexine.

The distribution of this character is unclear. The coding of Cunoniaceae is uncertain and needs TEM sections.

54. Vessels: 0 scalariform with many bars, 1 scalariform with few bars, 2 simple and scalariform with moderate to many bars, 3 simple and scalariform with few bars, 4 simple.

Scalariform perforation plates with many bars (0) appear throughout primitive angiosperms.

55. Imperforate type: 0 tracheids and/or fiber-tracheids with good bordered pits, 1 tracheids and fibers with bordered pits, 2 fibers with bordered pits, 3 fibers without bordered pits.

The first state (0) appears throughout primitive angiosperms.

56. Axile parenchyma: 0 diffuse, 1 banded, 2 both, 3 other.

Distribution of this character is unclear. *Ceratopetalum* is banded (1) and sometimes diffuse (0).

57. Rays: 0 heterogeneous, 1–3+ seriate, 1 heterogeneous, 1–2 seriate, 2 homogeneous, 1–2 seriate.

The first state (0) appears throughout primitive angiosperms.

58. *Ray crystals: 0 no, 1 yes.

Distribution of this character is unclear. The coding of *Acsmithia*, *Cunonia*, and *Pterocarya* for this character is not certain.

59. *Bract-bracteole complex off main axes: 0 yes, 1 only bract, 2 no.

Distribution of this character is unclear. *Ticodendron* is variable, either 0 or 1, and dependent on the sex of the inflorescence. The coding of *Acsmithia* and *Cunonia* is not certain.

60. *Bract-bracteole complex fused: 0 no, 1 yes, 2 Brunelliaceae NA.

The first state (0) appears throughout primitive angiosperms. *Ticodendron* is variable, either 0 or 1, and dependent on the sex of the inflorescence. The coding of *Acsmithia* and *Cunonia* is not certain.

61. *Main inflorescence axis: 0 branched (panicle, cymose), 1 simple unbranched (unbranched catkin, thyrse, raceme).

The first state (0) appears throughout primitive angiosperms. *Cunonia* is probably variable between the two states.

62. Structure in axile of bracteoles: 0 inflorescence axis (complex cyme), 1 flower, 2 *Ticodendron* variable, dependent on sex of inflorescence, 3 nothing, 4 *Davidsonia* NA.

The first state (0) appears throughout primitive angiosperms. *Cunonia* has a variable inflorescence (0) and flower (1), and *Castanea* is mostly with an inflorescence (0) and occasionally a flower (1).

63. Gynoecium: 0 apocarpous, lateral-admedial, 1 2 syncarpous and ascidate, carpel and attachment lateral-admedial, 2 2 syncarpous and ascidate, carpel and attachment apical, 3 3 syncarpous ascidate, attachment lateral and admedial, 4 2 syncarpous ascoplicate, lateral admedial, 5 2 syncarpous and ascidate, carpel and attachment basal.

The apocarpous state of the gynoecium appears throughout primitive angiosperms. The syncarpous state has a variable occurrence and appears to have multiple origins. (Terminology and distribution from Taylor, in press).

64. Ovule integuments: 0 apobitegmic, 1 apounitegmic, 2 hemiunitegmic, 3 hemibitegmic.

The apobitegmic state (0) appears scattered throughout primitive angiosperms. (Terminology and distribution from Taylor, 1988, in press.) Coding of *Brunellia*, *Acsmithia*, *Cunonia*, *Davidsonia*, *Nothofagus*, and *Alnus* is not certain.

65. Ovule morphology: 0 bitegmic, hemianatropous, 1 bitegmic, anatropous, 2 unitegmic, orthotropous, 3 unitegmic, hemianatropous, 4 unitegmic, anatropous.

The bitegmic, hemianatropous state (0) is common throughout primitive angiosperms. (Terminology and distribution from Taylor, 1988.) Coding of *Acsmithia*, *Cunonia*, *Castanea*, *Nothofagus*, and *Alnus* is not certain.

66. Stamen attachment and tip: 0 basal with apical extension, 1 basal without apical extension, 2 dorsiventrally fixed without apical extension, 3 dorsiventrally fixed with apical extension.

The first state (0) appears throughout primitive angiosperms. *Rhoiptelea* is either 0 or 1, and coding of *Davidsonia* and *Platycarya* is uncertain.

67. *Flowers: 0 bisexual or reduced bisexual, 1 unisexual.

The first state (0) appears throughout primitive angiosperms.

68. Perianth other than bract-bracteoles: 0 yes, two whorls, 1 no, 2 yes, one whorl.

Distribution of this character is unclear. *Ceratopetalum* is variable with character state 0 or 2 and *Fagopsis* is uncertain. We consider the vascularized papillae in *Myrica* to be perianth.

69. *Endosperm: 0 yes, 1 no or scanty.

The first state (0) appears throughout primitive angiosperms.

70. *Ovary: 0 superior, 1 inferior or semi-inferior.

The first state (0) appears throughout primitive angiosperms. Cunoniaceae coding is uncertain, and see perianth for *Myrica* coding.

SIEVE-ELEMENT CHARACTERS OF *TICODENDRON*[1]

H.-Dietmar Behnke[2]

Abstract

Among the families of Hamamelidae, *Ticodendron incognitum* Gómez-Laurito & Gómez P. contains S-type sieve-element plastids, the specifics of which (diameter and starch grains) would place it within or close to Betulaceae/Corylaceae. The absence of persistent, nondispersive P-protein bodies in the sieve elements of *Ticodendron* excludes the families of the Urticales and the Fagaceae, all regularly containing persistent P-protein bodies, from the list of its closest relatives.

Sieve-element characters, i.e., information obtained with the transmission electron microscope on sieve-element plastids, phloem proteins, and other morphological features, have largely been used to delimit higher taxa within angiosperms (Behnke, 1981a), but in a few cases were also helpful to assign single genera to a family (*Lophiocarpus*: Behnke, 1974; *Halophytum*: Hunziker et al., 1974; *Hectorella*: Behnke, 1975; *Swartzia*: Behnke, 1981b; *Geocarpon*: Behnke, 1982).

The hitherto unknown taxonomic position of the newly described genus *Ticodendron* (Gómez-Laurito & Gómez P., 1989a, b) and its probable relationships to various families of the Hamamelidae prompted an investigation of its sieve-element characters. Moreover, a survey of the sieve-element characters of all of the hamamelidaean families (Behnke, 1989) both facilitates a comparison with and asks for a complementation by data from *Ticodendron*.

Material and Methods

Shoot parts of a sapling of *Ticodendron incognitum* were collected in Costa Rica (*Bello & Haber 9809*), divided with a razor blade into longitudinal sections, and immediately immersed into a fixative containing paraformaldehyde and glutaraldehyde (Karnovsky, 1965). The samples were mailed to the author's laboratory, placed for 3 hr. in fresh Karnovsky's fixative, washed with 0.1 M sodium cacodylate buffer, postfixed for 1 hr. in 1% buffered OsO_4, dehydrated in acetone, embedded and polymerized in an Epon-Araldite mixture, and processed according to standard methods for ultrathin sectioning and eventual photographing with a transmission electron microscope.

Part of the prefixed material was dehydrated with ethanol, embedded into histowax, sectioned with a sliding microtome, stained with resorcin blue, and screened with a light microscope.

General Description of the Shoot

Transverse sections of the shoot sample studied show its composition as follows (cf. Figs. 1–3): the innermost part is occupied by the pith (Fig. 1: Pi) containing thin-walled parenchyma cells and large marginal, shizogenous secretory sacs surrounded by six epithelial cells (Fig. 1: ○). The length of these sacs, however, is restricted to about three to five times their width. The outermost pith cells, i.e., those bordering the xylem, often have lignified cell walls.

The xylem, phloem, sclerenchyma, and cortex make up distinct layers proceeding toward the periphery of the section. The shoot is protected by a periderm four to six cells broad (Fig. 1: Pe). The presence of a periderm, as well as the extent and the arrangement of xylem and phloem, demonstrate that this shoot part is already in its secondary growth period. The xylem (Fig. 1: X) shows a strict radial arrangement of its rather small and evenly sized cells interspersed by vessels, which may be twice as broad as the other elements but do not greatly disturb the radial array (Figs. 2, 3: X). Small multiseriate rays, in cross sections only one cell broad, are found at regular intervals. In a few parts of the studied shoot sample, the phloem (Figs. 1, 2: P) reflects its origin from radially aligned

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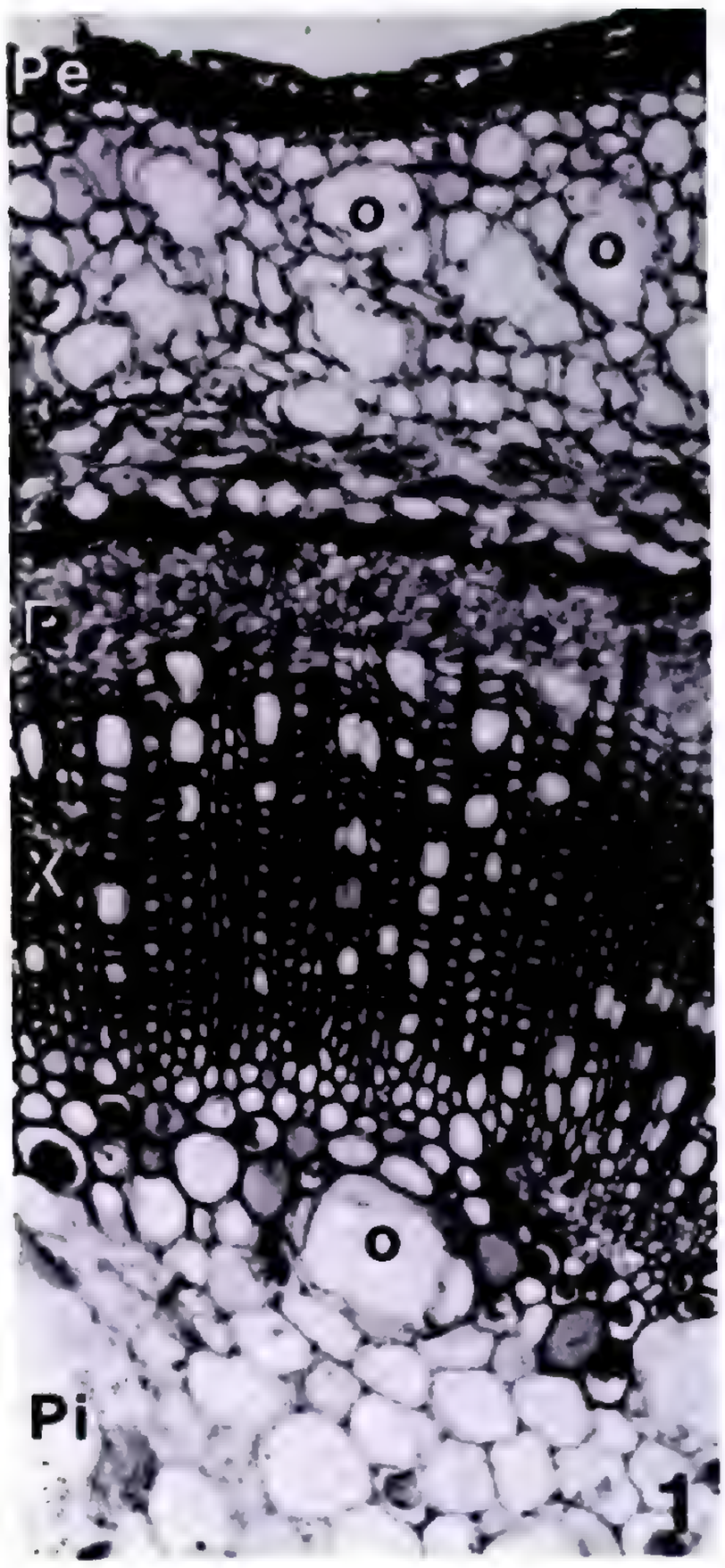

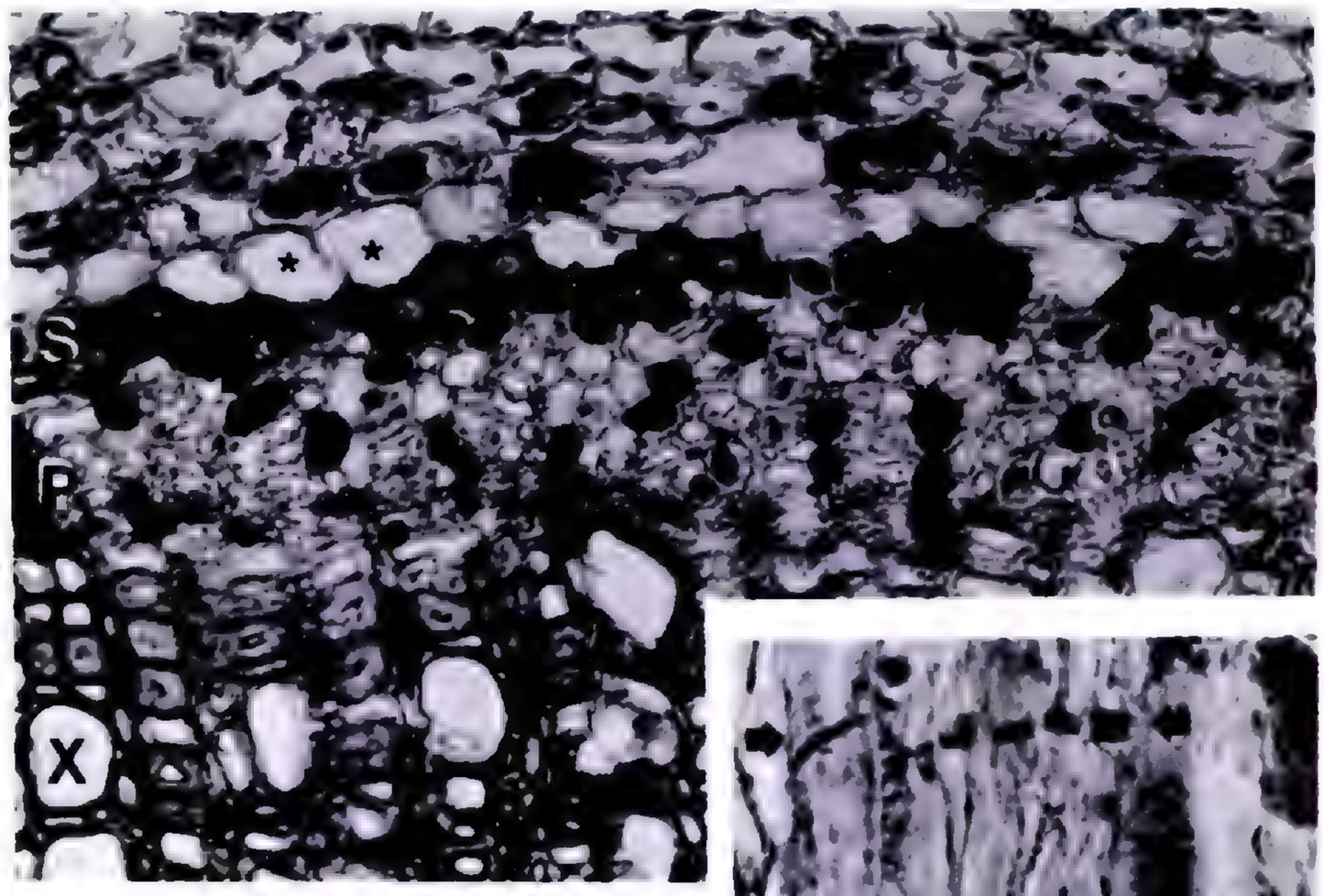

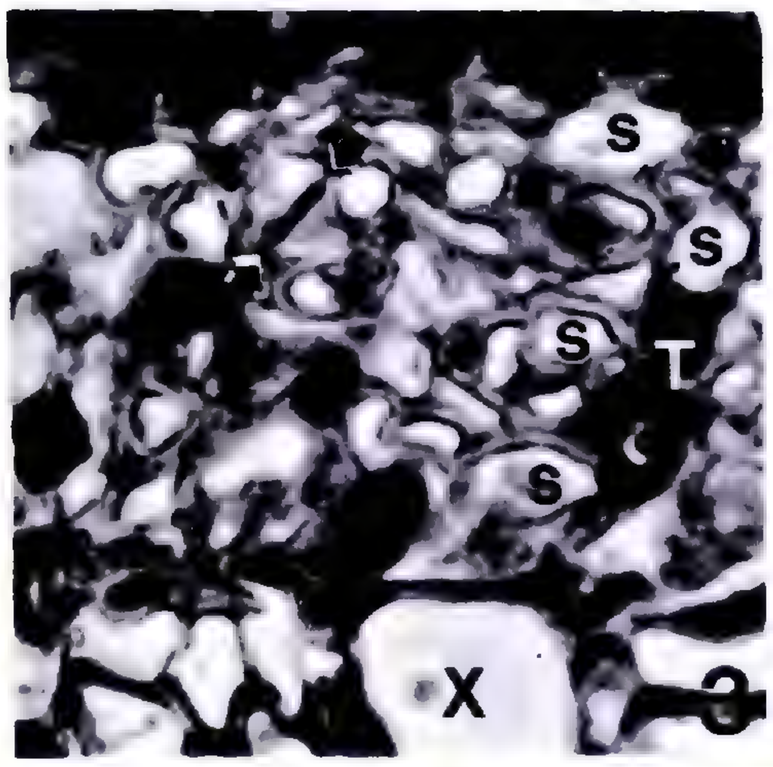

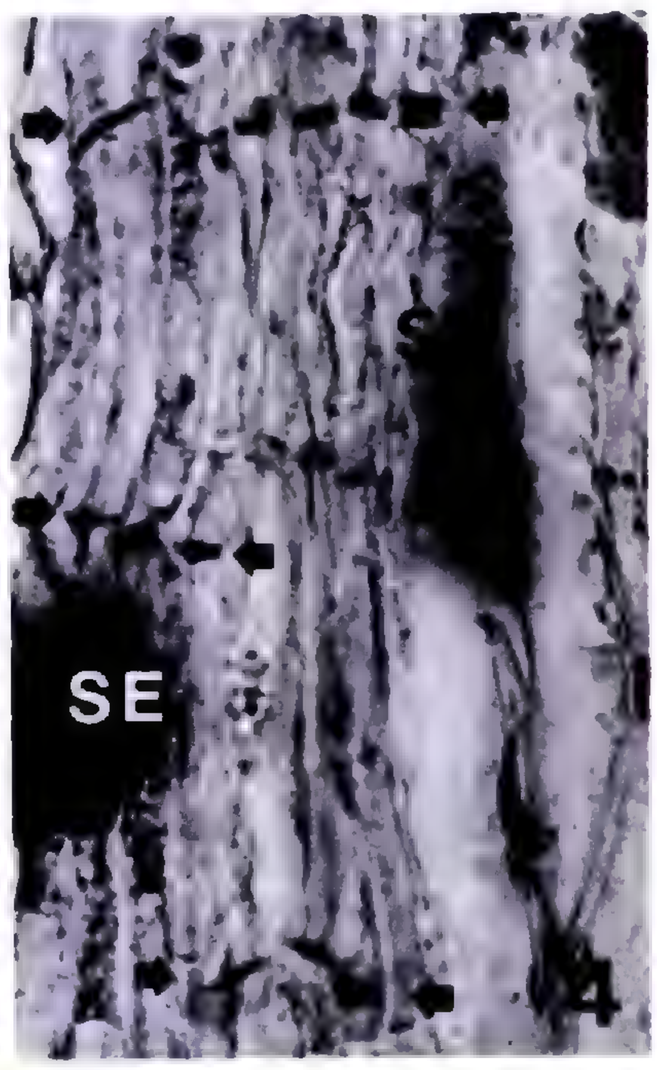

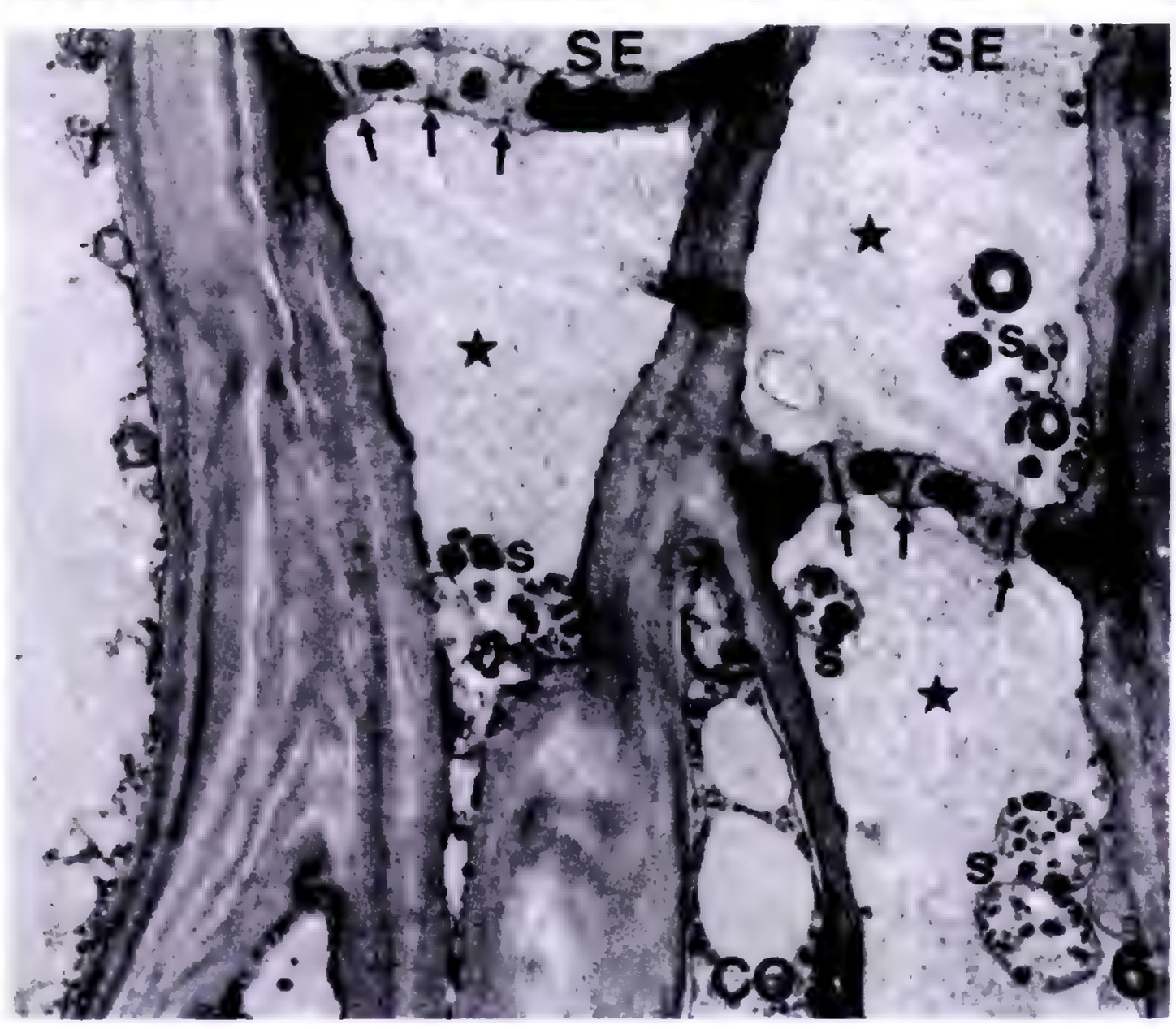

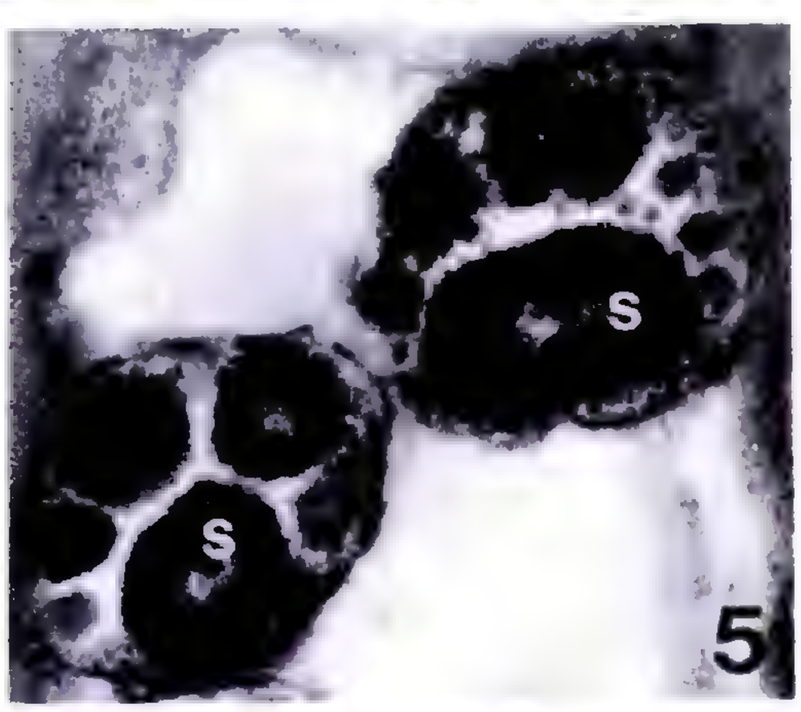

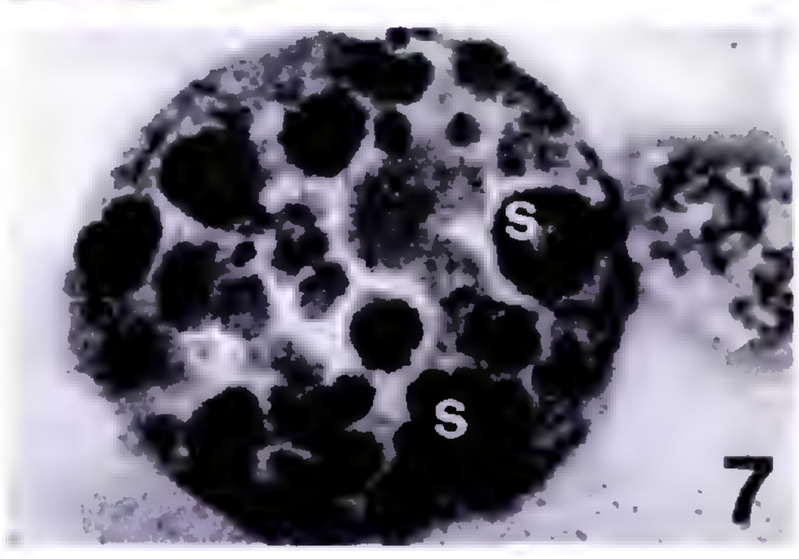

FIGURES 1–7. *Ticodendron incognitum*. — 1. Cross section of young shoot with periderm (Pe), cortex (C), phloem (P), xylem (X), and pith (Pi). Cortex and pith contain secretory elements (o); ×100. — 2. Detail of cross-sectioned vascular cylinder showing part of secondary xylem with vessels (X), phloem delimited against the cortex by sclerenchyma (S), and a pericycle made up of transparent cells (*); ×230. — 3. Part of cross-sectioned phloem with numerous thick-walled sieve elements (s) and black tannin cells (T); oblique sieve plate between arrows; ×500. — 4. Longitudinal section through phloem with many parallel-aligned sieve elements (SE) with sieve plates between arrows; ×570. — 5, 7. S-type sieve-element plastids with many small to medium-sized starch grains (s); ×30,000. — 6. TEM longitudinal

cambial initials. The cambial layer itself is rather small and difficult to delimit.

The sclerenchymatous sheath (Fig. 2: S) consists of mostly one layer of thick-walled fibers, but longitudinal sections indicate that thinner-walled stone cells do occur rather frequently, probably bridging the gaps between different fiber groups. A one-celled pericyclic layer of clear parenchymatic cells adjoins the sclerenchyma toward the periphery of the shoot (Fig. 2: *).

The cortex is composed of small parenchyma cells and numerous large secretory cells (Fig. 1: C, ○). Compared to the pith secretory sacs, these are much shorter, their extension being almost the same in all directions.

The content of the pith and cortex secretory elements seems to be mucilaginous. In addition, small cells containing tanninlike substances (Fig. 3: T) are frequently found in the cortex and are also present in all other tissues (see black cells in Figs. 1–3). Crystal cells (containing clustered crystals) are abundant in the cortex but are also frequent in the phloem and in the lignified pith cells, which border the innermost xylem.

Sieve-element Characters

The phloem of *Ticodendron* is composed of sieve elements (Fig. 3: s), companion cells (Fig. 6: CC), and phloem parenchyma cells. Comparatively many of the parenchyma cells, including those in phloem rays, contain tanninlike substances (Fig. 3: T)

With a diameter of 6–10 μm, sieve elements of *Ticodendron* are very narrow; their length is about 80–100 μm. Secondary sieve elements are somewhat smaller than primary ones and are more regularly aligned (see Fig. 4 with sieve plates aligned between arrows). Sieve plates are commonly restricted to the end walls and have their pores arranged in a single sieve area (simple sieve plate). The position of the sieve plate is in general at right angles to the lateral wall, and only in some cases is much inclined (Fig. 3, between arrows). The pore diameter is about 0.5 μm (Fig. 6, arrows), mostly occluded by heavy callose collars (due to unfavorable conditions during tissue preparation of the sample used).

As seen with the transmission electron microscope, sieve elements have comparably thick walls and are enucleate when mature. Plastids and mitochondria are about the only organelles present and reside at the periphery of the cells, whereas filaments of P-protein are dispersed throughout the sieve element (Fig. 6: ⋆) and are also trapped within the sieve pores.

The sieve-element plastids contain starch grains only and thus belong to the S-type. Their average diameter is about 1 μm, and they contain an average of eight round or ovoid starch grains. However, there is much size variation among *Ticodendron* sieve-element plastids (compare Figs. 5 and 7); diameters range from 0.7 to 1.5 μm.

No persistent or nondispersive P-protein bodies were found in the investigated sample. All mature sieve elements screened contained P-protein, the filaments of which were more or less evenly dispersed over the cell lumina (Fig. 6: ⋆).

Comparison of the *Ticodendron* Sieve-element Characters to Those of Putatively Related Taxa

The sieve elements of *Ticodendron* contain S-type plastids as do the great majority of dicotyledons, including all of the hamamelidalean families (Behnke, 1981a, 1989). The plastids of *Ticodendron* are smaller (1.0 μm) than the total average of S-type plastids (1.4 μm, based on 1,400 S-type species). The families that contain S-type plastids with an average diameter between 1.2 and 0.8 μm include 12 of the 28 families of putative hamamelid alliance, five of the six families making up the Fagales and all of those in the Urticales (Behnke, 1989).

Variation in the morphological features of the starch grains of *Ticodendron* falls outside that of the families of Urticales; their starch grains are larger and fewer (compare Figs. 6 and 7 with figs. 6.5 and 6.6 in Behnke, 1989). Also, with the exception of the Cannabaceae, all of the Urticales sieve elements contain a specific globular nondispersive P-protein body (see fig. 6.1 in Behnke, 1989), lacking in *Ticodendron*.

Among the families of Fagales, the Nothofagaceae differ by their larger-sized plastids and the Fagaceae by their compound-spherical nondispersive protein bodies found in all species studied so far. Betulaceae and/or Corylaceae would have the

←
section through part of phloem with two sieve elements (SE) and a companion cell (CC). The sieve elements contain many S-type plastids (S) and evenly dispersed filaments of P-protein (⋆). Sieve pores (arrows) are almost totally occluded by callose deposits (white wall parts) and arranged into simple sieve plates; ×5,000.

closest similarities in their sieve-element characters. The Betulaceae s.l. (e.g., in the sense of Cronquist, 1981, or Takhtajan, 1987) have S-type plastids with an average diameter of 1.2 μm and about five medium-sized starch grains. If Corylaceae are held to be a separate family (e.g., Dahlgren, 1989), their plastid characters (diameter 1.1 μm; about eight starch grains) would fit nicely with those of *Ticodendron*. However, considering the comparatively wide range of measurements on which averages are based, none of the discussed families would seem inappropriate.

Based on its sieve-element data, *Ticodendron* would fit best within Betulaceae/Corylaceae, if only hamamelid families are considered. It is obvious that a positive alignment of *Ticodendron* cannot be given on only sieve-element characters; these characters can only be used to favor or exclude proposals for a taxonomic position made on account of many other characters.

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REPRODUCTIVE MORPHOLOGY, ANATOMY, AND RELATIONSHIPS OF *TICODENDRON*[1]

Hiroshi Tobe[2]

ABSTRACT

Ticodendron is predominantly dioecious. Both male and female inflorescences bear some cymules (or partial inflorescences) on their primary axes. Male partial inflorescences are borne verticillately in clusters of three, each being one- to three-flowered and subtended by a single bract. Staminate flowers have 8–10 or more stamens and lack a perianth. Female partial inflorescences are solitary. Each of them is always one-flowered, although it is subtended by three (one primary and two secondary) bracts, and it produces some scales in each axil of the secondary bracts. In pistillate flowers, concentric bundles are prevalent in the periphery of the pistil wall; the ovary is inferior, bicarpellate, and four-locular with one ovule in each locule; the placentation is axile; the ovules are apical, pendulous, hemitropous, unitegmic, and crassinucellate; the integument is 20–30 cells thick and vascularized by about 20 longitudinally parallel vascular bundles; and the mature seeds have a two-cell-layered endosperm and seed coats composed of thick-walled integumentary cell layers and vascular tissues. In reproductive morphology *Ticodendron* is distinct from any other family but is best placed in Fagales. On the basis of evidence from reproductive morphology and from other sources it is suggested that *Ticodendron* appears to have diverged early from a common ancestor with Betulaceae or Fagaceae.

Ticodendron, comprising only *T. incognita*, which occurs from northern Nicaragua through Costa Rica to central Panama, has long been a mystery plant because of its uncertain identity (Gómez-Laurito & Gómez P., 1989; Hammel & Burger, 1991). The present paper provides a detailed description of floral morphology and anatomy of *Ticodendron* including a few remarks on its embryology, in order to shed light upon the position and affinity of the genus.

MATERIALS AND METHODS

All examined materials were collected at Monteverde, Costa Rica, and fixed with FAA; examined were nearly mature male flowers (*Haber 7072*), young female buds and fruits (*Gómez-Laurito s.n.* in 1986; *Haber 6840, 6868, 7286*). Voucher specimens are deposited at MO and CR.

For anatomical study, single flowers, groups of male and female flowers, and a piece of mature seed were sectioned with a rotary microtome following standard paraffin methods. Before being sectioned, the materials were softened with a mixture of 10 parts of glycerol, 3 parts of 10% Aerosol OT, and 90 parts of water (Schmid & Turner, 1977) as described in Tobe & Raven (1984). Sections cut at 6–10 μm thickness were stained with Heidenhain's hematoxylin, safranin, and fastgreen FCF.

OBSERVATIONS

Ticodendron is mostly dioecious. Male and female inflorescences both appear to be spikes. However, on the basis of anatomical observations discussed later, it has been found that the "spike" is composed of some one- to three-flowered cymules borne on the primary axis. To facilitate discussions in comparing *Ticodendron* with other related taxa, a more comprehensive term, "partial inflorescence" (instead of "cymule"), will be used in the following descriptions (see Abbe, 1974: 164–165, for terminology).

MALE PARTIAL INFLORESCENCES AND FLOWERS

Male partial inflorescences are borne verticillately on the inflorescence axis in clusters of three (Fig. 1). Each male partial inflorescence is subtended by a single primary bract, and is composed of 1–3 staminate flowers basically arranged in a

[1] I am grateful to Jorge Gómez-Laurito, Barry Hammel, and William A. Haber for collection of fixed materials, to Michael H. Grayum and Luis Diego Gómez for valuable information on *Ticodendron* and related taxa in earlier stages of the work, and to Peter H. Raven for support in various ways.

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dichasium. Individual partial inflorescences (as well as individual staminate flowers in the case of three-flowered partial inflorescences) are not readily distinguished from each other, but their distinctness is revealed by vascular bundles. Those supplying each partial inflorescence or each staminate flower depart in separate groups from the vascular cylinder of the inflorescence axis. Staminate flowers have 8–10 or more stamens and lack perianth and pistil, or rarely they have an abortive pistil (see arrow, Fig. 1).

The stamens are tetrasporangiate, and the anthers dehisce longitudinally. Anther walls comprise a fibrous endothecium and a persistent epidermis at maturity. Pollen is two-celled when shed.

FEMALE PARTIAL INFLORESCENCES AND FLOWERS

Female partial inflorescences are solitary, and each is always one-flowered, although it is subtended by one primary and two opposite secondary bracts. These three bracts may fuse basally (Fig. 6B). At each axil of the secondary bracts, some 10 small appendages or scales are produced, each receiving a distinct vascular bundle (Fig. 2). These scales are horizontally scattered in the axil and are attached at somewhat different levels.

Pistillate flowers are composed only of a single inferior ovary with a small, inconspicuous perianth on the top of the ovary (Fig. 3). The flowers rarely have abortive stamens on the inner side of the perianth; the abortive stamens receive a distinct vascular bundle as do ordinary ones. The ovary is bicarpellate with two (rarely three) elongate separate styles and four-locular, each locule containing one ovule (Fig. 4). Styles are stigmatic throughout with elongate and papillate epidermal cells. A narrow adaxial sulcus is present on styles throughout. Judging from the position of the two styles in relation to the inflorescence axis (see Fig. 6C, I), the two carpels are positioned tangentially, not radially.

The floral vascular anatomy of a female flower is presented in Figure 6, which diagrammatically shows the vascular course in a longitudinal section (Fig. 6A) and in selected serial transverse sections (Fig. 6B–I). At and above the level at which the scales are supplied with vascular bundles (Fig. 6B, C), the vascular cylinder, which is composed of many discrete collateral bundles arranged in a ring, irregularly diverges into the peripheral vascular system and the central vascular system (Fig. 6D, E).

The peripheral vascular system is about 15 or 16 aggregates of 4–10 small bundles. Included are a few inverted ones throughout the whole length of flower (Figs. 5, 6D–H). This peripheral vascular system supplies the perianth (and abortive stamens, if present) and the styles (Fig. 6F–I). Each style has three (occasionally four) vascular bundles (Fig. 6I).

The central vascular system is composed of some 20 small collateral bundles, which ascend as placental bundles to supply the ovules (Fig. 6E, F). Ovule placentation is axile.

OVULES

Although pistillate flowers were collected simultaneously with nearly mature staminate ones, the oldest ovules were still in the megaspore dyad stage. Probably more than several weeks pass between pollination and fertilization. The oldest ovules available indicate that the ovule is apical, pendulous, and hemitropous with the micropyle upward, and that it twists somewhat as it grows (Fig. 7). The ovule is crassinucellate. By the megaspore dyad stage, about 4–5 parietal cells lie above the dyad (Fig. 8). Obturators are lacking.

The ovule is unitegmic (Fig. 7), with the integument about 20–30 cells thick and with its tips forming a long narrow micropyle. The integument is vascularized by some 20 longitudinally parallel vascular bundles (Fig. 9), which are derived from a raphe bundle via its post-chalazal branching. The integument is longitudinally ribbed, each rib containing a single vascular bundle (Figs. 9, 10). Outer epidermal cells of the integument are radially elongate and contain rich cytoplasm (Fig. 10).

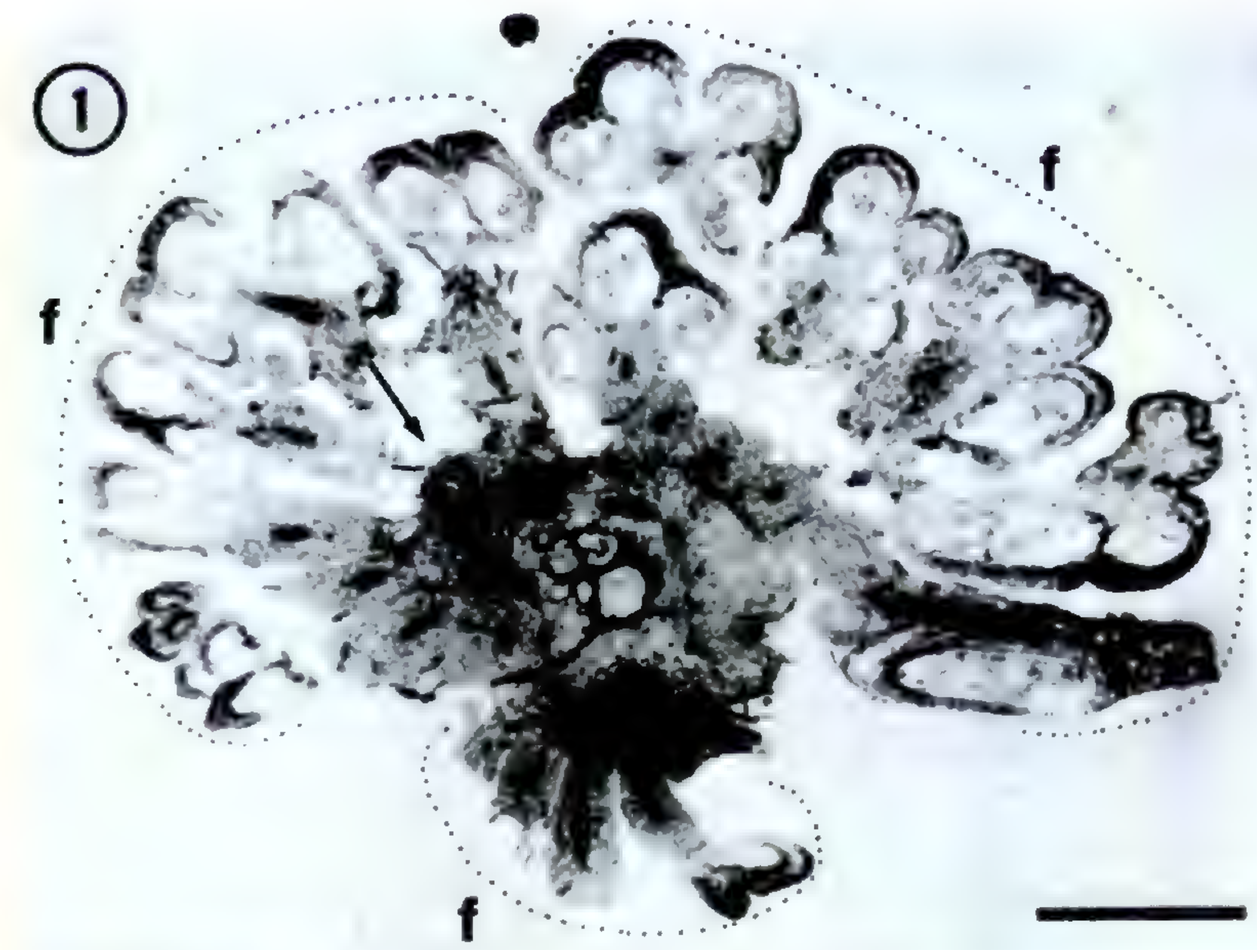
MATURE SEEDS

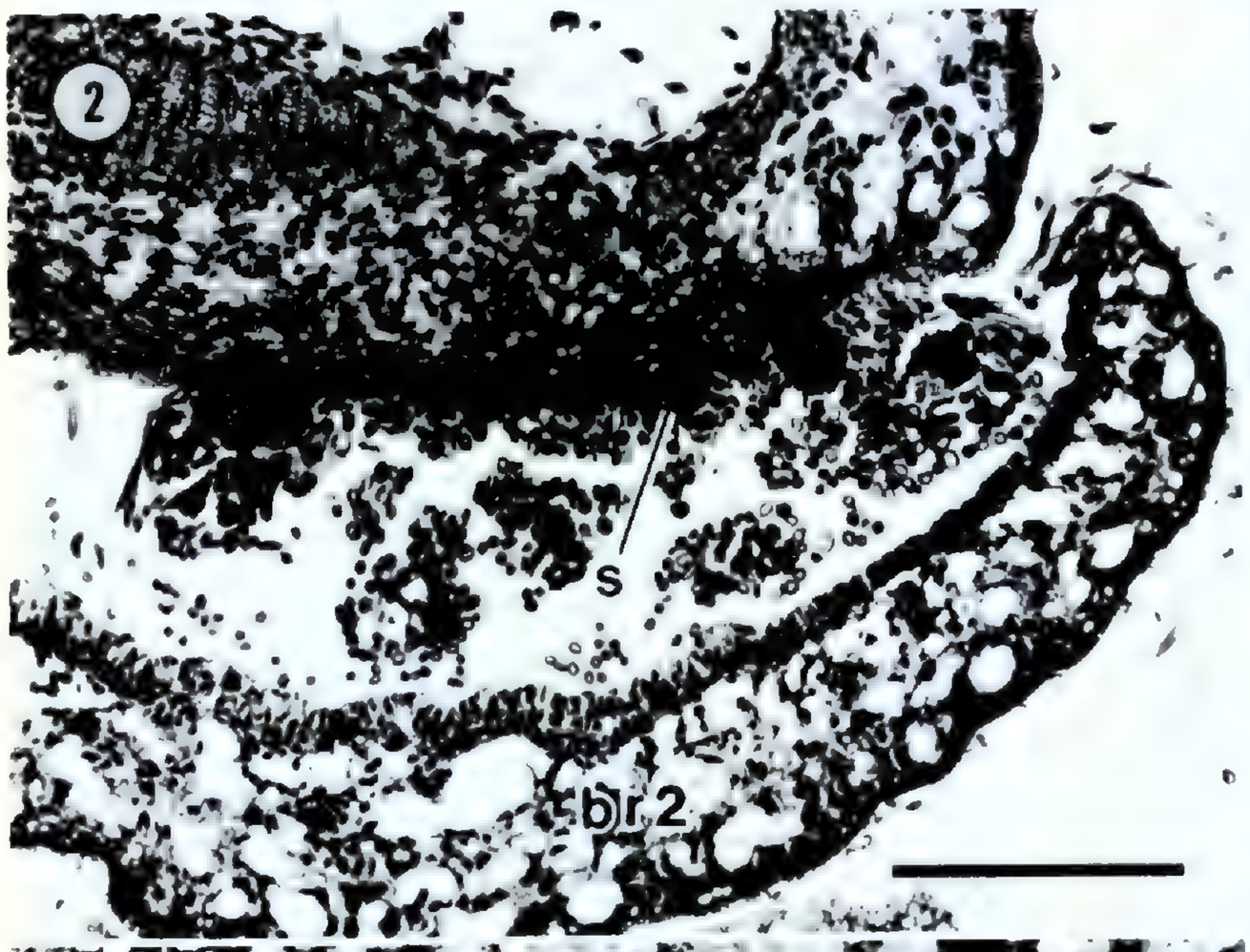
Only one of the four ovules in the ovary develops into a mature seed, thus each mature fruit is one-seeded. The embryo of a mature seed is oily and massive with two straight cotyledons. The mature seed has a two-cell-layered endosperm (Fig. 11).

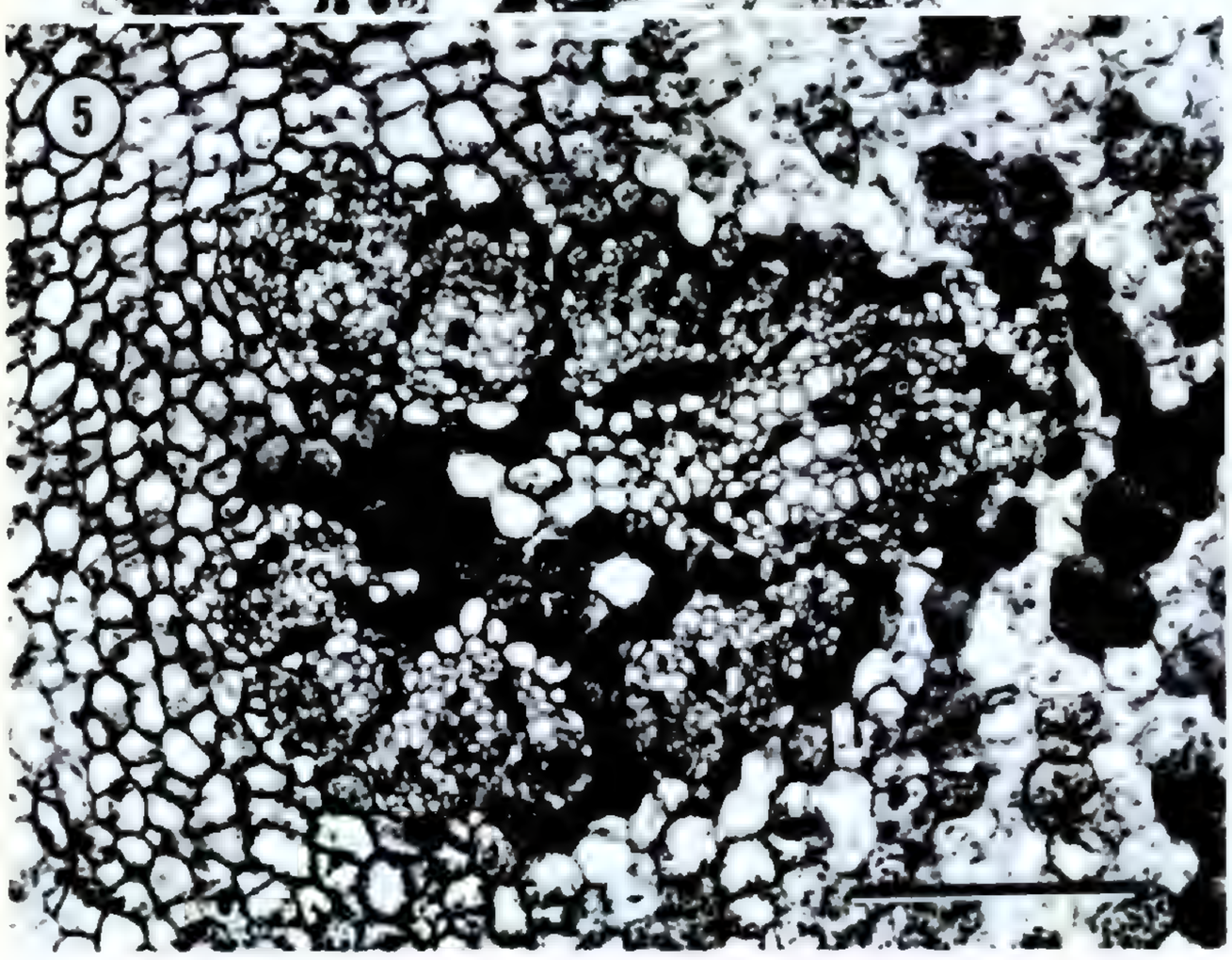
As the seed matures, only the outer tissue of the integument, including a vascular tissue and a surrounding integumentary tissue, persist, while the inner tissue completely degenerates. Thus, the mature seed coat is only about 8–15 cells thick (Fig. 11). Those cells, except for xylem cells of the vascular tissue, are thick-walled and flattened with tanninlike contents. The outer epidermal cells of the integument, which were radially elongate and contained rich cytoplasm in ovular stages, do not show any specialization in the mature seed coat.

DISCUSSION

The above-described inflorescence and floral structures of *Ticodendron* fit within the range of







FIGURES 1–5. Anatomy of partial inflorescences and flowers of *Ticodendron*. —1. Transverse section (TS) of a primary male inflorescence axis showing three male, one-flowered partial inflorescences. Arrow indicates abortive pistil. —2. TS at the base of female partial inflorescence. Note that some scales are borne at the axil of the secondary bract. —3. Longitudinal section of female partial inflorescence, which is always one-flowered. —4. TS of female flower at level of pistil. —5. TS of concentric bundles prevalent in the periphery of the female flower. Abbreviations: br2, secondary bract; f, single male flower; ov, ovule; pe, perianth; s, scale; sy, style. Scale bars equal 1 mm, 500 μm, 1 mm, 1 mm, and 100 μm, respectively.

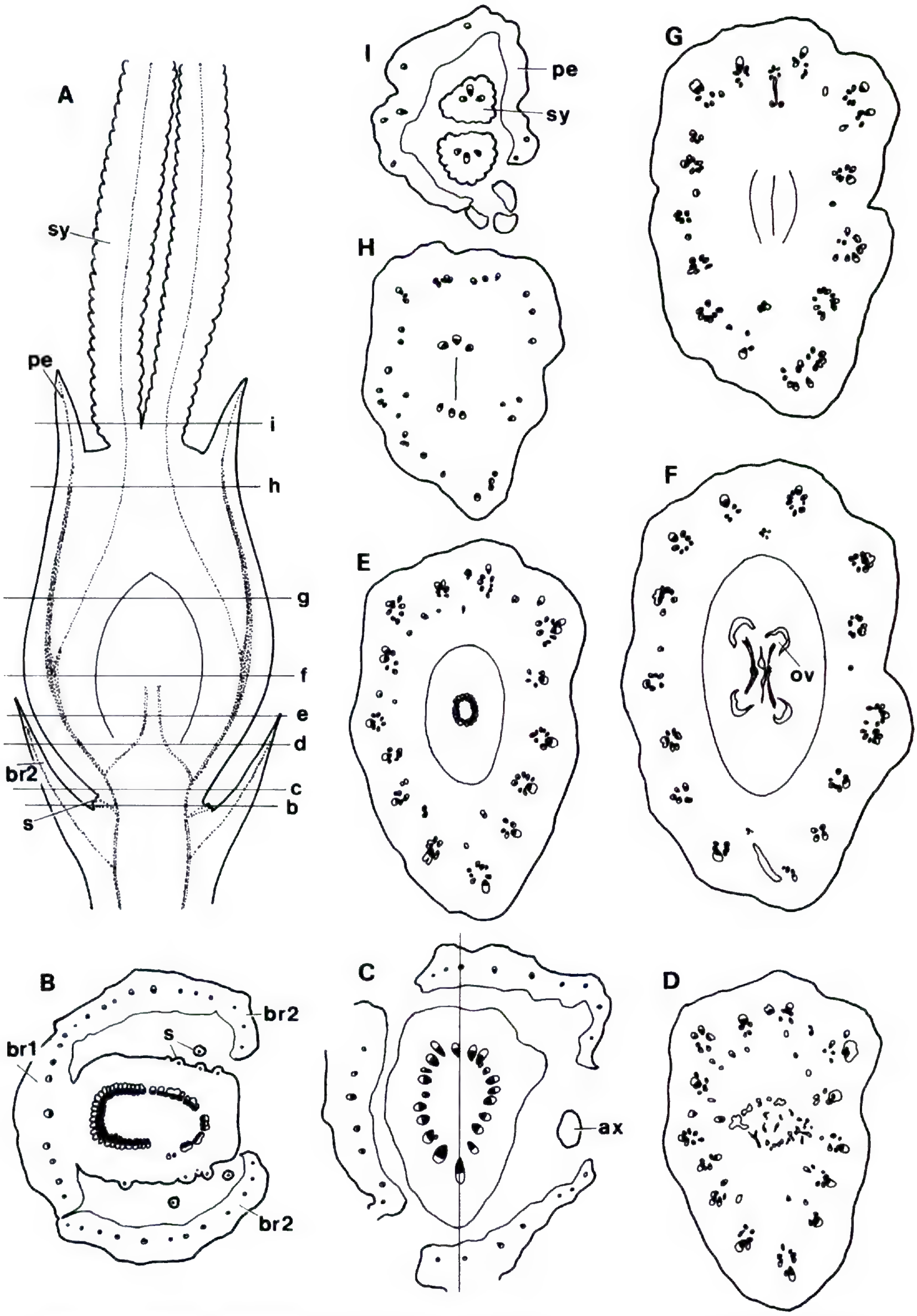
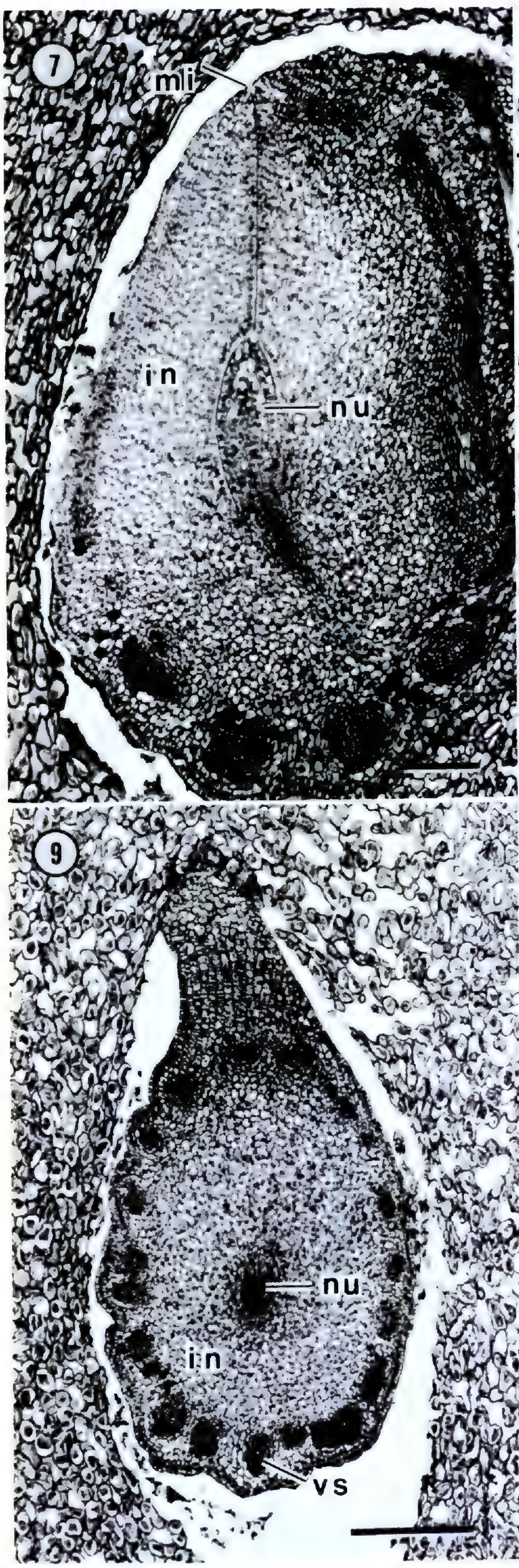
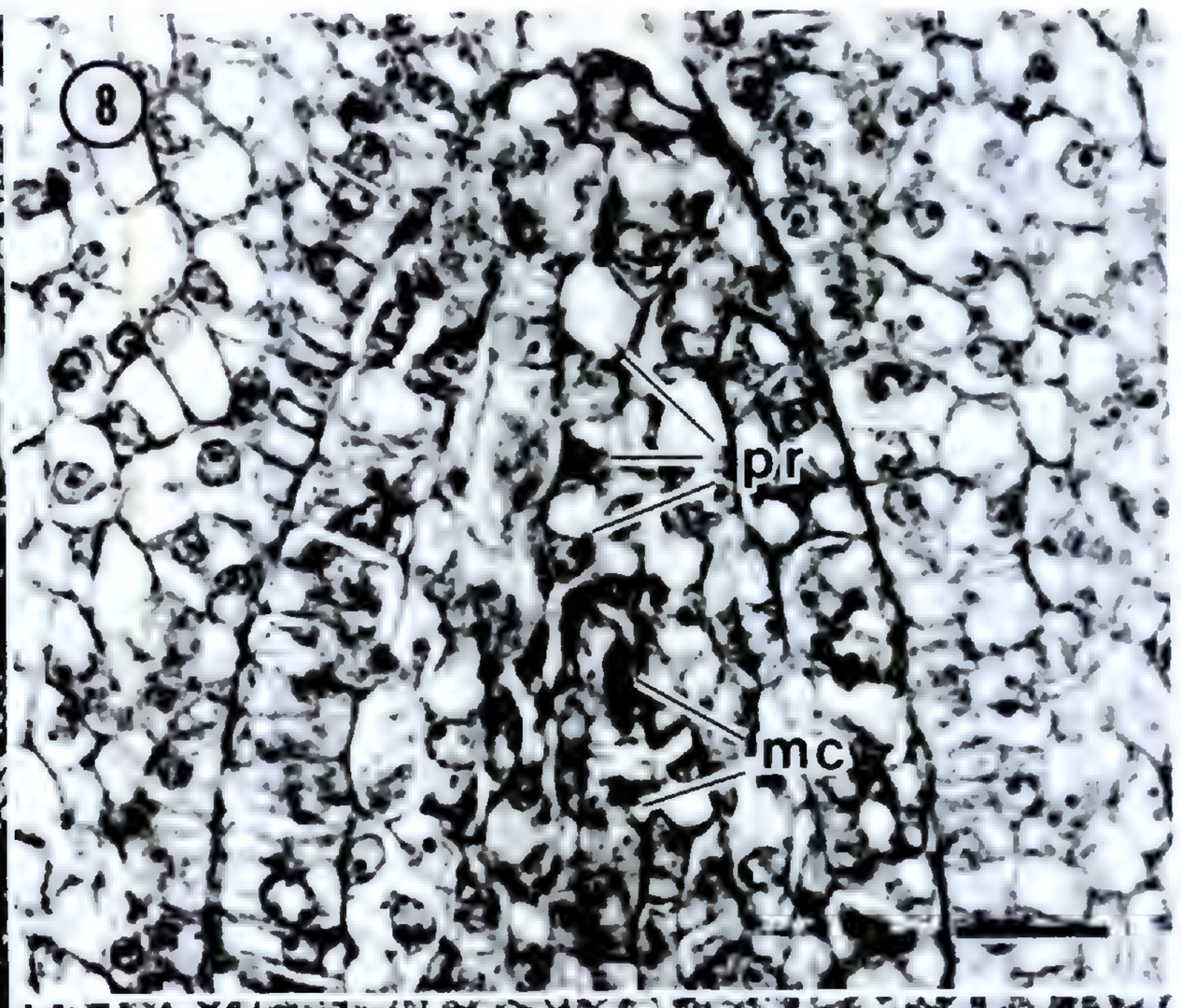
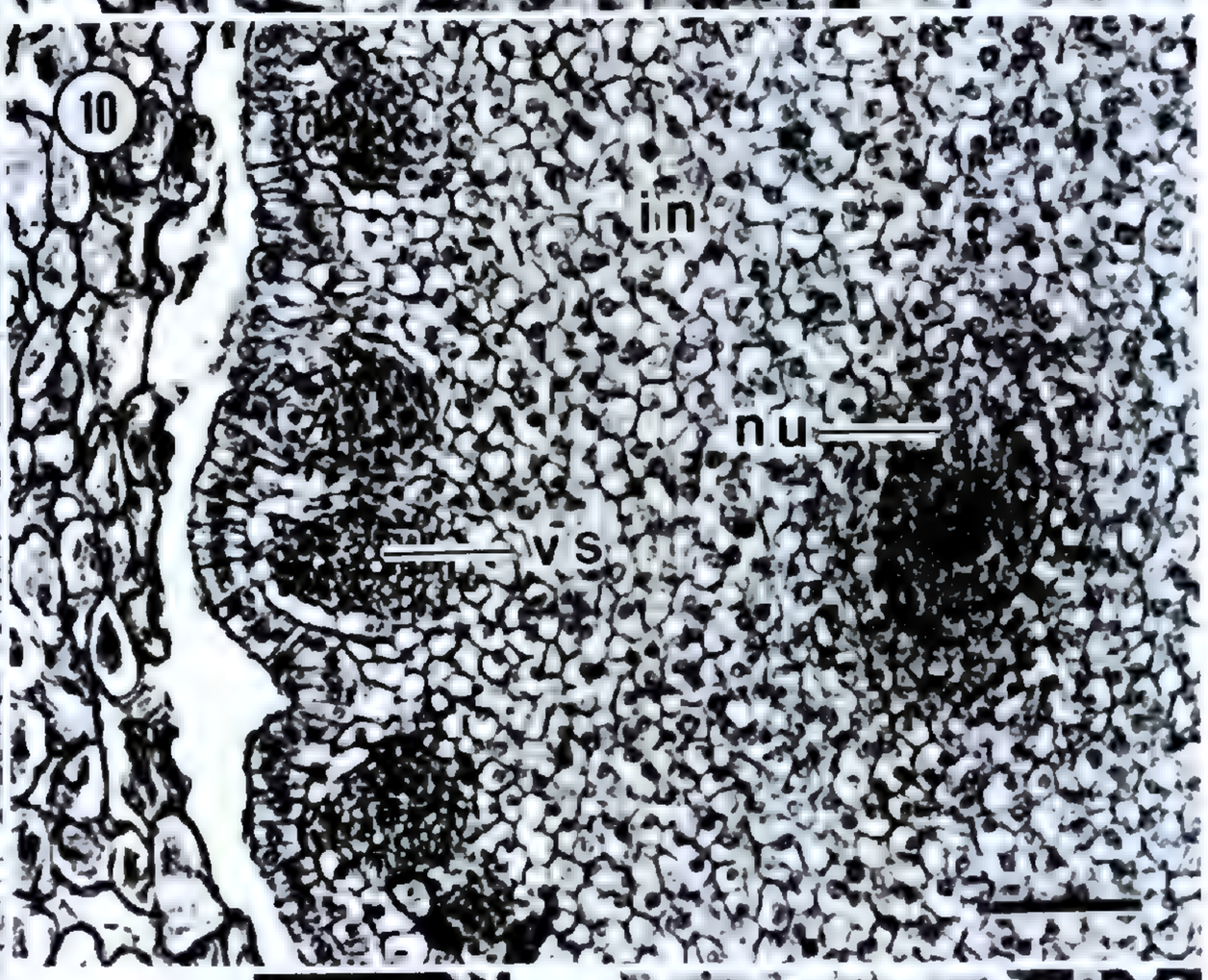
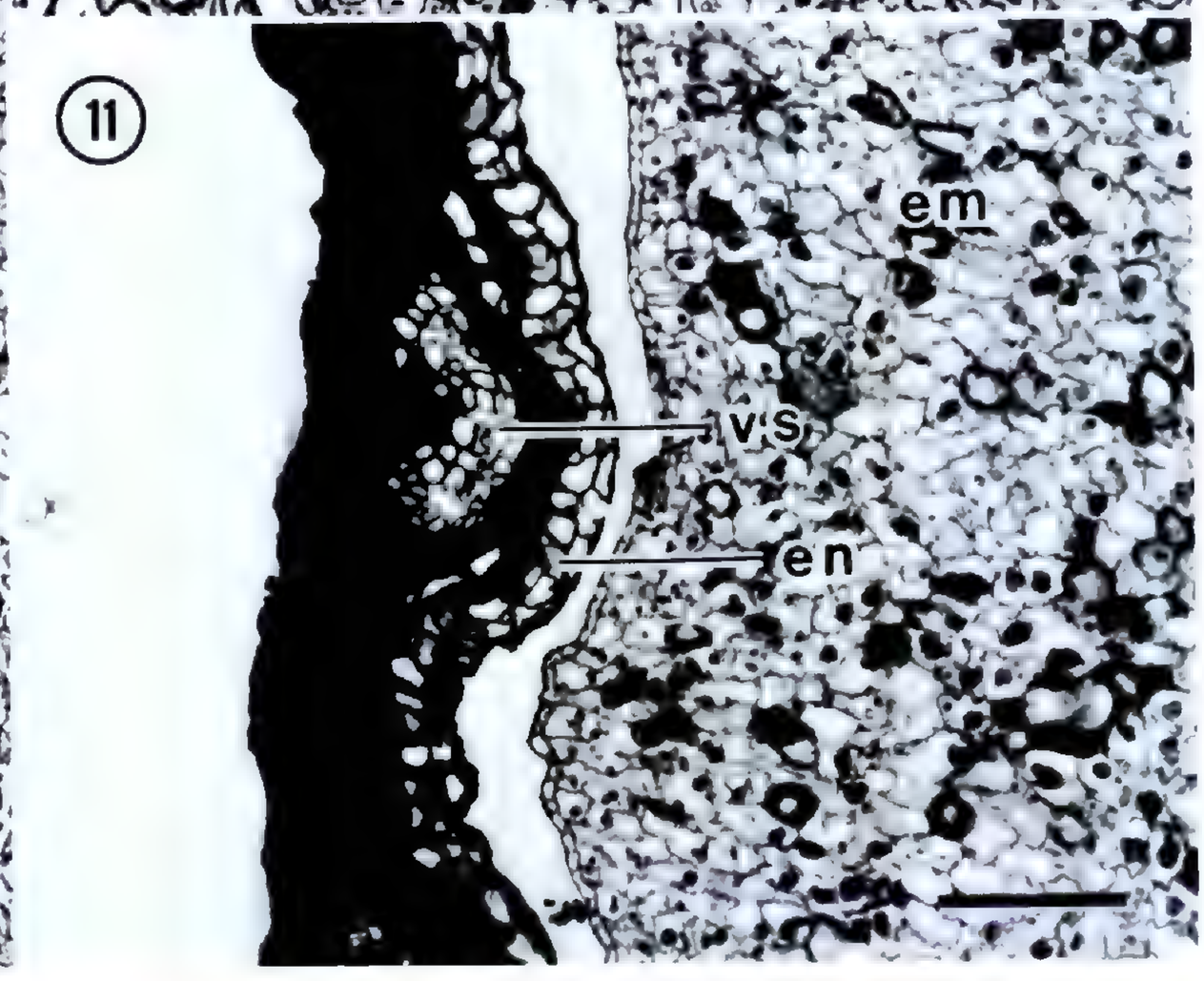


FIGURE 6. Diagrams illustrating the vascular anatomy of female partial inflorescence and flower in *Ticodendron*. — A. Median longitudinal section through the line presented in C. B–I. Transverse sections at levels marked b–i in A. Abbreviations: ax, suppressed primary inflorescence axis; br1 and br2, primary and secondary bracts; ov, ovule; pe, perianth; s, scale; sy, style.









FIGURES 7–11. Anatomy of ovules and seeds in *Ticodendron*.—7. Longitudinal section (LS) of ovule.—8. LS of ovule showing a dyad of megaspores in a nucellus.—9. Transverse section (TS) of ovule showing that the integument is ribbed and contains a vascular bundle in each rib.—10. Enlargement of part of Figure 9, showing a structure of thick integument.—11. TS of mature seed showing seed coat structure. Abbreviations: em, embryo; en, endosperm; in, integument; mc, megaspore; mi, tip of micropyle; nu, nucellus; pr, parietal cell; vs, vascular bundle. Scale bars equal 100 μm, 20 μm, 200 μm, 200 μm, and 100 μm, respectively.

TABLE 1. Comparisons of *Ticodendron* with related families in selected reproductive characters.

Characters[1]	*Ticodendron*	Fagaceae (Fagales)	Betulaceae (Fagales)	Juglandaceae (Juglandales)	Myricaceae (Myricales)
Cupule	Absent	Present	Absent	Absent	Absent
Ovary position	Inferior	Inferior	Inferior	Inferior	Superior
Concentric bundles in pistil wall	Present	?	Present	Present	?
Number of carpels per ovary	2	(2)3(−12)	2(3)	2(−4)	2
Number of locules in ovary	4	(2)3(−12)	2(3)	1	1
Number of ovules in ovary	4	(4)6(−many)	2–4(−6)	1	1
Ovule position	Axile, pendulous	Axile, pendulous	Axile, pendulous	Axile, erect	Basal, erect
Ovule curvature	Hemitropous	Anatropous	Anatropous	Orthotropous	Orthotropous
Number of integuments	1	(1)2	1(2)	1	1
If unitegmic, thickness of integument	20–30 cells thick	4–5 cells thick	4 cells thick	6–10 cells thick	3–7 cells thick
Vascular bundles in integument	Present	Present	Present	Present	Present
Ribbed integument	Present	Absent	?	Absent	?
Mature seed coat	Cells thick-walled	Cells thick-walled	?	Cells thick-walled	?
Thickness of endosperm	2 cells thick	Absent or 1 cell thick	2–4 cells thick	1 cell thick	1 cell thick

[1] References are: Netolitzky (1926), Vaughan (1970), and Corner (1976) for all families (seed coat anatomy); Langdon (1939, 1947) and Poole (1952) for Fagaceae; Wolpert (1910) for Betulaceae; Karsten (1902), Langdon (1939), Meeuse & Houthuesen (1964), Verhoog (1968), and Manning (1978) for Juglandaceae; and Kershaw (1900), Kühn (1927), and Yen (1950) for Myricaceae.

variation for these features shown in Fagales, Juglandales, and Myricales (see Abbe, 1974, for review) and suggest closer affinity of *Ticodendron* with these orders than with other Hamamelididae or members of different subclasses. In Table 1, reproductive features of *Ticodendron*, Fagales, Juglandales, and Myricales are presented.

In general, *Ticodendron* agrees well with Fagales, Juglandales, and Myricales. They share an inferior ovary (except Myricales with a superior ovary), concentric bundles in floral vascular system (though uncertain in Betulaceae and Myricales), bicarpellate ovaries (though frequently tricarpellate in Fagales and Juglandales), unitegmic ovules (commonly bitegmic in Fagales), vascular bundles in the integument (in the outer integument only in Fagales with bitegmic ovules), a similar mature seed coat composed of numerous thick-walled cell layers and vascular tissues, and a thin endosperm in mature seed. *Ticodendron* further coincides with Fagales in having two (or more) ovules per carpel and axile placentation, rather than a uniovulate ovary with basal placentation as in Juglandales and Myricales. *Ticodendron* agrees with Myricales in having a longitudinally ribbed integument.

Thus, the reproductive morphology and anatomy of *Ticodendron* indicates a close relationship to Fagales, Juglandales, and Myricales in the Hamamelididae (or "Hamamelidae" sensu Cronquist, 1981). Among Fagales, Juglandales, and Myricales, *Ticodendron* seems to be more at home within Fagales, which have diverse reproductive morphology, rather than in Juglandales or Myricales, both of which are characterized by certain unique apomorphies. Juglandales and Myricales both characteristically have a unilocular bicarpellate ovary with a single orthotropous ovule, all features that are unknown in *Ticodendron* and Fagales. Closer affinities of *Ticodendron* with Fagales are further suggested by evidence from wood anatomy, pollen morphology, and other data, as specified in this volume.

Among Betulaceae, Coryleae may be the closest allies of *Ticodendron*, since Coryleae, like *Ticodendron*, lack a perianth in the male flowers but possess it in the female flowers. Evidence from wood anat-

omy also suggests Coryleae for the closest affinity of *Ticodendron* (Carlquist, 1991). Yet, in *Ticodendron* the ovule is hemitropous with a thicker integument (20–30 cells thick), whereas in Coryleae it is anatropous and probably with a thinner integument (e.g., four cells thick in *Betula*; Wolpert, 1910); *Ticodendron* has scales at the axils of the secondary bracts, which are unknown in Coryleae (and in all other Betulaceae); *Ticodendron* lacks the tertiary bracts that are positioned decussate to the secondary bracts and form by their fusion a characteristic involucre or hull in Coryleae (Abbe, 1935, 1938, 1974); in *Ticodendron* stamens are not deeply divided as in Coryleae (and in all other Betulaceae); and in *Ticodendron* female flowers are solitary, while in Coryleae two lateral flowers of the dichasium usually develop (Abbe, 1935, 1938, 1974). These differences suggest that *Ticodendron* is unlikely to have direct relationships with Coryleae or other Betulaceae.

Nothofagus is the best candidate in comparing Fagaceae with *Ticodendron*. In fact, *Nothofagus* is superficially similar to *Ticodendron* in having exclusively unitegmic ovules, occasionally solitary staminate flowers, partial inflorescences composed of 1–3 pistillate flowers, and occasionally bicarpellate pistillate flowers (for data on *Nothofagus* see Langdon, 1947; Poole, 1952; Abbe, 1974). *Ticodendron*, however, is clearly distinguished from *Nothofagus* (and in general from all other Fagaceae) in having hemitropous ovules with thicker integument (only four or five cells thick in *Nothofagus*; Poole, 1952) and in lacking characteristic cupular valves, lacking a perianth in male flowers, and lacking the tertiary bracts in female partial inflorescences. Those dissimilarities seem to indicate that *Ticodendron* clearly stands out from Fagaceae as well.

Balanopaceae (*Balanops* only), which have been placed by Cronquist (1981, 1988) in Fagales, may also require comparisons with *Ticodendron*. *Balanops* shares with *Ticodendron* a female partial inflorescence comprising a single pistillate flower subtended by a "cupule," an ovary with locules, an anatropous, unitegmic ovule, and drupaceous fruits. However, the "cupule" of *Balanops* is composed of numerous, spirally arranged, deltoid bracts, lacking an elevated axial structure characteristic of Fagaceae (Hjelmqvist, 1948). Its homology with the cupule of Fagaceae is doubted (Cronquist, 1981). Even if the bracts of the "cupule" of *Balanops* are comparable with the scales of *Ticodendron*, the former encloses the whole of the pistillate flower, while the latter is restricted only at the axils of the secondary bracts. *Balanops* is clearly distinct from *Ticodendron* in having a basal, erect ovule and lacking a perianth in the pistillate flower. Hjelmqvist (1948) suggests on the basis of comparison in the "cupule" structure that *Balanops* probably stands nearest Juglandales and Myricales. Carlquist (1980) notes that the wood of *Balanops* is comparable with that of Hamamelidaceae. Zavada & Dilcher (1986) indicate on the basis of similarity cluster analysis using pollen characters that *Balanops* is a sister group of *Nothofagus*. At the present level of our knowledge it is uncertain even whether *Balanops* is related with Fagales in general. *Balanops* is poorly known with respect to many reproductive structures, and an intensive and overall investigation on the genus seems to be desired prior to critical comparisons with putative allies and *Ticodendron*.

In considering evolutionary relationships with Betulaceae and Fagaceae, the presence of the scales in the secondary bract axils of female partial inflorescences of *Ticodendron* may have a key role. Although 1–3-(or 7- or more-)flowered partial male and female inflorescences are prevalent in Betulaceae and Fagaceae (see Abbe, 1935, 1938, 1947), they are generally considered to have evolved from a more complex cymose inflorescence by reduction of branches of higher orders (see Abbe, 1938, 1974). Indeed, reduced outer sterile branches are elaborated as cupular valves in Fagaceae (Fey & Endress, 1983); furthermore, vestigials of presumably reduced outer sterile branches appear as "supernumerary scales" in male partial inflorescences of *Chrysolepis chrysophylla* (Fagaceae) (Hjelmqvist, 1948) or as blinding vascular bundles in female partial inflorescences of *Betula lenta* (Betulaceae) (Abbe, 1935). Although it is uncertain whether the scales of *Ticodendron* are directly relevant to the scales of the cupule of *Nothofagus* or not, their anatomical features are very similar to each other in their cross sectional shape and in receiving a distinct vascular supply (see Langdon, 1947, for cupule-scale anatomy in *Nothofagus*). The scales of the female partial inflorescence of *Ticodendron* may also represent residuals of reduced outer sterile branches of cymose inflorescences.

Regarding nonreproductive characters, Carlquist (1991) showed that *Ticodendron* has primitive wood compared with other Fagales; Feuer (1991) observed that pollen of *Ticodendron* had plesiomorphic (tectate-granular) wall structure shared with Betulaceae, *Nothofagus*, Casuarinales, and Urticales (see Zavada & Dilcher, 1986); and Hickey & Taylor (1991) suggested, on the basis of leaf architectural analysis, that *Ticodendron*

took a more basal position than other Fagales (and Brunelliaceae). *Ticodendron* may be considered an early derivative either from a common ancestor of Fagaceae before the reduced outer sterile branches of the cymose inflorescence were elaborated as the cupular valves, as in modern Fagaceae, or from a common ancestor of Betulaceae before the reduced outer sterile branches were lost completely, as in modern Betulaceae. For more critical discussion of relationships, embryological studies in *Ticodendron*, *Nothofagus*, and Betulaceae, which are still meager compared with those in other genera or families, are needed.

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POLLEN MORPHOLOGY AND THE SYSTEMATIC RELATIONSHIPS OF *TICODENDRON INCOGNITUM*

Sylvia Feuer[1]

ABSTRACT

Pollen of *Ticodendron incognitum*, a monotypic Central American tree of uncertain affinity, was examined in detail with the hope of clarifying the relationships of this taxon. Pollen of *Ticodendron* is isopolar to subisopolar due to the slight displacement of the apertures toward one of the poles, slightly rounded-convex, suboblate, and triporate with slightly aspidote pores. Exine sculpturing is minutely spinulate with the spinules clustered and restricted to short rugulate ridges. The exine is organized into an evenly thickened tectum exhibiting narrow channels and perforations, a columellate/granular interstitium composed of prominent columellae typically pendent from the tectum and coarse sporadic granules, and an unevenly thickened continuous foot layer. In apertural areas the exine is composed only of tectum and pendent columellae and granules. The foot layer terminates approximately 3 μm from the external pore opening. Pollen data, particularly sculpturing and the nature of the interstitial elements, offer strong support for placement of *Ticodendron* among the "higher" Hamamelidae with close ties to the Myricales and Casuarinales.

Ticodendron incognitum Gómez-Laurito & Gómez P., a dioecious or polygamodioecious Central American tree, has recently been described as a new genus and species with uncertain affinities (Gómez-Laurito & Gómez P., 1989). Based on morphology, anatomy, embryology, and leaf architecture, *Ticodendron* has been linked to the "higher" Hamamelidae sensu Cronquist (1981) (Urticales, Casuarinales, Fagales, Myricales, and Juglandales) and to the Dilleniidae. Pollen of *Ticodendron* has been examined in detail and compared to that of the above-mentioned orders in the hope of clarifying the relationships of this genus.

MATERIALS AND METHODS

Fresh pollen fixed in FAA from the collection *Haber 7072* (MO) was acetolyzed and divided into portions for viewing with the light microscope (LM), scanning electron microscope (SEM), transmission electron microscope (TEM), and in cryosection (cryo-SEM).

Pollen for LM was mounted in glycerine jelly and photographed with a Nikon-UFX system at 500× using Agfapan (ASA 25) black and white film developed in 1 : 25 Rodinal.

Pollen for SEM was freeze-dried, gold-coated, and viewed with an ISI DS-130 microscope.

Pollen for TEM was osmicated in 1% aqueous osmium tetroxide for two hours, washed several times in distilled water, and embedded in 1.5% purified agar. The pollen/agar moiety was minced into cubes smaller than 1 mm, dehydrated through acetone, and embedded in Araldite 6005 resin. Sections were cut with a diamond knife, collected on 75 × 300 uncoated grids, stained with uranyl acetate and lead citrate, and viewed with a JEOL 1200 EX microscope.

Pollen for cryosection was prepared according to methods outlined in Feuer (1987), which involved mounting a pollen/agar block onto a cryosectioning stub, surrounding the block with Tissue-Tek® and freezing the stub with liquid nitrogen. The sections were cut with an American Optical Cryo-cut freezing microtome at 10 μm thicknesses and picked up on cover slips. The cover glasses were then placed in double-distilled boiling water to dislodge the sections and remove the agar/Tissue-Tek® medium. Cryocut pollen was rinsed several times in boiling double-distilled water, centrifuged, and prepared for standard viewing in the SEM.

Pollen ultrastructural terminology follows that of Faegri & Iversen (1964) in the use of ektexine and endexine, and Walker & Walker (1981) in the use of interstitium.

Families included in the comparative pollen discussion follow the system of Cronquist (1981) except for the maintenance of the Celtidaceae and Ulmaceae as distinct families. Palynological com-

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TABLE 1. Palynological comparisons between *Ticodendron* and extant families.

Ticodendron	*FAG*	*DIL*	*ACT*	*BAR*	*BAL*	*URT*	*MOR*	*ULM*	*CEL*	*CAN*	*RHO*	*JUG*	*CAS*	*MYR*	*BET*
Isopolar to subisopolar	−	−	−	−	−	−	−	−	−	−	−	+	+	+	+
Suboblate shape range	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+/−
Porate	−	−	−	−	−	+	+	+	+	+	−	+	+	+	+
Aspidote	−	−	−	−	−	−/+	+	+	+	+	−	+	+	+	+
Minutely spinulate sculpturing	−	−	−	+/−	+	+	+	+	+/−	+	+	+	+	+	+
Spinules solitary, in single file, on short rugulate ridges	−	−	−	−	−	0	−	−	−	−	−	−	+	−	+
Ektexine only	−	−	−	−	−	0	−	?	?	?	−	−/+	−	+	+/−
Tectum with narrow, radial microchannels	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+
Interstitium well-defined	+/−	+	+	+	+	0	+	+	+	+	+	+	+	+	+
Interstitium columellate granulate	−	−	+	−	+	0	−	−	+/−	+	+	+/−	−	+	+/−
Columellae coarse, irregularly thickened, prominent	−	+	−	+	+	0	−	−	+/−	−	−	−	+	+	−
Columellae often pendent	−	−	−	0	−	0	−	−	−	−	−	+	+	+	+
Foot layer continuous	−/+	+	+	−	−	0	0	−	−	+	+	+	+	+	+
Foot layer unevenly thickened	+	+	+	−	+	0	0	−	−	0	+	−	+	−	−/+
Aperture without foot layer	−	−	−	+	−	0	0	0	0	0	+	+	+	+	+/−
Aperture composed of only pendent ektexinous elements	−	−	−	0	−	0	0	0	0	0	+	+	+	+	+/−
Total shared characters	3	4	4	4	5	5	6	6	8	8	9	13	14	14	15

Key to abbreviations and symbols: FAG (Fagaceae), DIL (Dilleniaceae), ACT (Actinidiaceae), BAR (Barbeyaceae), BAL (Balanopaceae), URT (Urticaceae), MOR (Moraceae), ULM (Ulmaceae), CEL (Celtidaceae), CAN (Cannabaceae), RHO (Rhoipteleaceae), JUG (Juglandaceae), CAS (Casuarinaceae), MYR (Myricaceae), BET (Betulaceae).

+/−, −/+ character present in some of the taxa; predominant character listed first.

0 no data available.

? conflicting data.

parisons between *Ticodendron* and extant taxa are listed in Table 1 in order of increasing palynological similarity to *Ticodendron*.

Pollen Description

Ticodendron incognitum (Figs. 1–11).

Symmetry: radial. *Polarity*: isopolar to subisopolar; subisopolarity due to slight displacement of apertures toward one polar face. *Size*: polar $\bar{X}$ = 22.7 μm (21.3 μm–24.5 μm); equatorial $\bar{X}$ = 27.3 μm (25.2 μm–30.7 μm). *Shape*: *amb* triangular slightly rounded-convex; suboblate, rarely oblate-spheroidal. *Apertures*: three, rarely four pores; pores small, $\bar{X}$ = 3.4 μm (2.6 μm–4.5 μm), slightly aspidote; exine thickening near apertures. *Sculpturing*: tectate-perforate, minutely spinulate; spinules typically restricted to short rugulate ridges bearing 3–5 spinules, spinules rarely occurring singly; perforations minute, circular, numerous, clustered. *Exine structure*: only ektexine present. *Nonapertural ektexine* organized into tectum, interstitium and foot layer. *Tectum*: evenly thickened, thick (0.5 μm–0.7 μm) continuous with solid, acute-tipped minute spinules (0.2 μm–0.3 μm), tectum 0.30 μm–0.35 μm thick in nonspinulate areas, exhibiting narrow, radial channels often continuous through entire width of tectum. *Interstitium*: well-defined, 0.4 μm–0.8 μm thick; columellate/granulate, columellae numerous, clustered, undulate, in section often appearing pendent from the lower surface of the tectum and rarely fusing with foot layer, irregularly thickened, occasionally bifurcating at the base or fusing laterally in the upper half of the interstitium; granules sparse, spherical, coarse, variable in size, occurring sporadically throughout interstitium. *Foot layer*: unevenly thickened, continuous, upper surface uneven, lower surface smooth. *Apertural ektexine*: in an area approximately 3 μm in diam. surrounding the pore: (1) interstitium thickening slightly composed of larger and longer pendent columellae and numerous granular elements; granules clustered along lower surface of the interstitium; (2) foot layer absent, abruptly terminating after a slight thickening and lamellation at the periphery of this region; and (3) pore opening encircled by a ca. 1 μm rim of solid thickened exine resting on a narrow, finely granular zone. In the light microscope, exine thinning in equatorial areas adjacent to pores. Ratio of tectum and interstitium to foot layer: 5 : 1 in nonspinulate areas.

Discussion

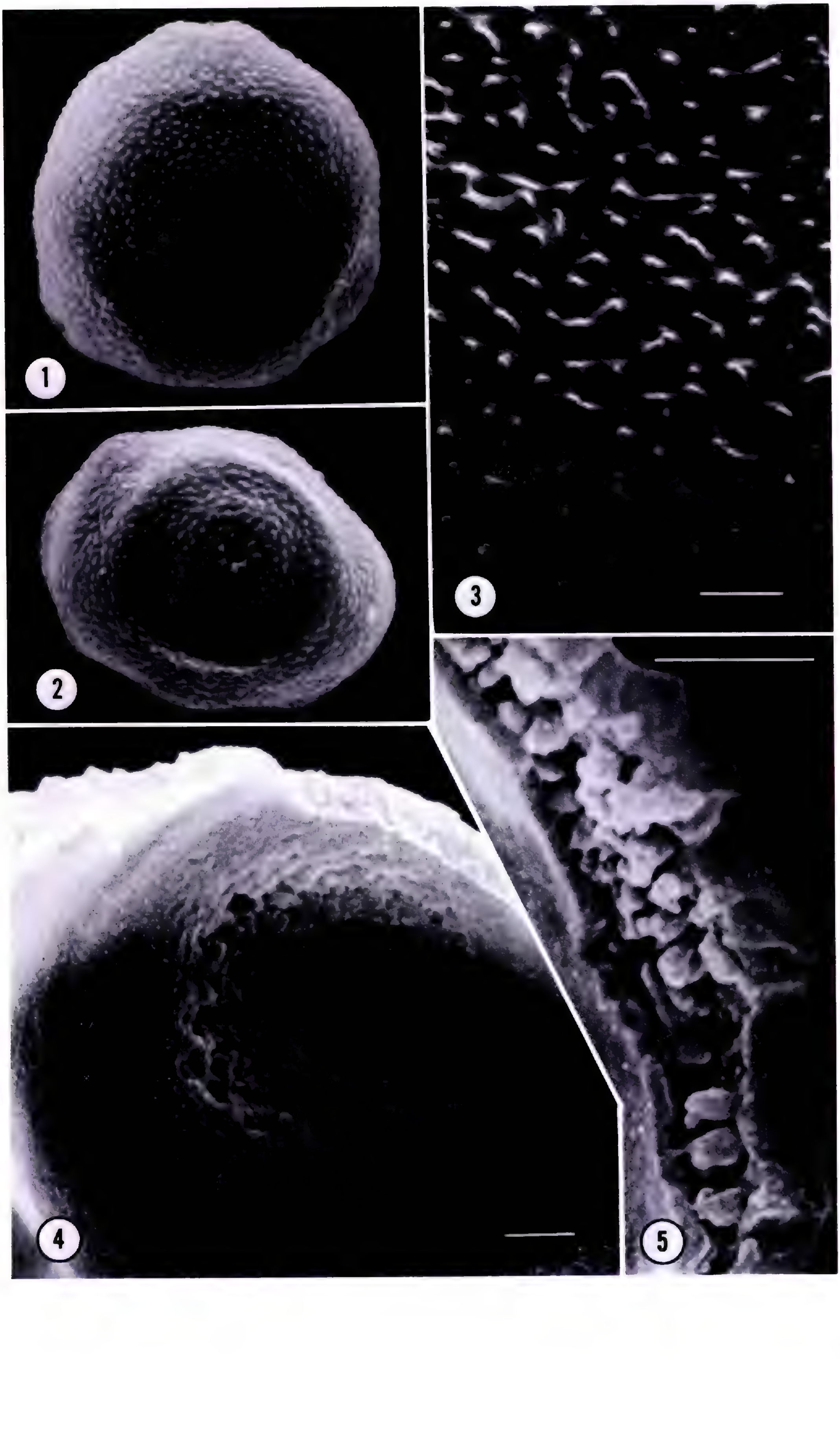
The following sections compare pollen characters of *Ticodendron* to members of the Fagales, Dilleniideae, Urticales, Juglandales, Casuarinales, and Myricales as well as to the fossil pollen form group Normapolles. Palynological comparisons of *Ticodendron* to extant orders are discussed from least to most similar.

Fagales (Balanopaceae, Fagaceae, excluding Betulaceae)

From the available description and one published TEM micrograph by Zavada & Dilcher (1986), pollen of the monotypic Balanopaceae differs from that of *Ticodendron* in aperture number, aperture type, and in several key features of the exine. Pollen of Balanopaceae is 3–5-colpate with a columellate/granulate interstitium. The columellae are short, irregularly thickened, and sporadic with the apical portions interconnected by a narrow, infratectal granular zone composed of randomly fused granules arranged just below the tectum. Unlike *Ticodendron*, endexine is prominent and continuous around the grain.

Pollen of Fagaceae is even more distinct from pollen of *Ticodendron* than are the Balanopaceae. Excluding *Nothofagus* (see below), pollen of Fagaceae is tricolporate to rarely tricolporoidate and prolate-spheroidal, and spinulate sculpturing does not occur. Sculpturing ranges from coarsely to finely scabrate to striato-rugulate to papillo-verrucate to entwined rodlets. The exine is organized into an irregularly thickened, highly perforate tectum, a strictly columellate interstitium and a prominent, often discontinuous, foot layer. Endexine is continuous around the grain with a gradual, slight thickening near the aperture (Crepet & Daghlian, 1980; Praglowski, 1982).

The 3–10-stephanocolpate pollen of *Nothofagus* with its uniquely raised apertural margins and narrow granular interstitium is also very different from pollen of *Ticodendron*. Though pollen of *Nothofagus* and *Ticodendron* are both spinulate, spinules in the former are twice as large, sparsely distributed, solitary, and often extend through the tectum to project into the interstitium. Unlike *Ticodendron*, the coarsely granular interstitium in *Nothofagus* exhibits no columellar elements and the endexine is thick, continuous around the grain, and abruptly and significantly thickened at the aperture (Praglowski, 1982).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DILLENIALES
(DILLENIACEAE S.S., ACTINIDIACEAE)

Dilleniaceae and *Ticodendron* have very different pollen. Pollen of Dilleniaceae extends into the subprolate shape range and is tricolpate, tetracolpate, tricolporate to inaperturate with typically psilate, perforate to reticulate sculpturing. Though the tectum is perforate as is *Ticodendron*, the perforations are numerous and broad. The interstitium in Dilleniaceae, though well-defined, is composed of large, numerous, uniform columellae resting on a thick foot layer. Endexine is continuous around the grain and is particularly well-developed at the aperture (Dickison et al., 1982).

Pollen of Actinidiaceae is also very different from that of *Ticodendron*. Pollen is tricolporate with specialized exine bridges associated with the endoaperture. Pollen shape extends into the prolate range, the sculpturing is psilate to scabrate, and the exine is composed of a highly perforate tectum, a thick continuous foot layer, and endexine continuous around the grain and prominent at the aperture. The interstitium in Actinidiaceae is columellate/granulate to granulate, and uniquely highly undulate due to an irregularly thickened foot layer (Dickison et al., 1982).

URTICALES (BARBEYACEAE,
URTICACEAE, MORACEAE, ULMACEAE,
CELTIDACEAE, CANNABACEAE)

Relatively little is known palynologically about the major families Moraceae (ca. 1,000 species) and Urticaceae (ca. 700 species), but the available pollen data indicate significant differences between pollen of most Urticales and *Ticodendron*. Urticalean pollen is typically di-, stephano-, periporate or rarely tricolporate with scabrate sculpturing or minute spinules clustered together on small raised islands of exine. Ultrastructurally, the interstitium in Ulmaceae is spongy, characterized by randomly anastomosing strands of ektexine or columellate/granulate in the Celtidaceae and Moraceae with thin columellae interspersed among the granules. The foot layer is extremely thin in most taxa and absent in Barbeyaceae (Zavada, 1983). Conflicting data are available on the presence of endexine in Celtidaceae and Ulmaceae. Endexine has not been reported in the Ulmaceae or Celtidaceae by Zavada (1983), though it appears to be present in Zavada's illustration of *Parasponia* (Celtidaceae) (fig. 11 in Zavada, 1983). In contrast, Takahashi (1989) reported endexine in both the Celtidaceae and Ulmaceae. Endexine has been found in Barbeyaceae and Cannabaceae, but in the latter its occurrence is still problematic. Zavada & Dilcher (1986) described endexine in their familial pollen description, but in Appendix II of the same paper, which details the coding of character states used in their phylogenetic analysis, endexine is coded as absent in Cannabaceae.

Of the Urticales examined to date, the Cannabaceae are palynologically the most similar to *Ticodendron*. The grains in this family are triporate with aspidote apertures and spinulate sculpturing. In thin section (TEM), the tectum is irregularly thickened, channeled, and the interstitium is largely columellate (Zavada & Dilcher, 1986). Though Cannabaceae and *Ticodendron* exhibit a similar overall organization of the interstitium, the details of these elements are quite different. Columellae in Cannabaceae are short, thin, typically apically and basally flared and consistently attached to both the tectum and foot layer.

JUGLANDALES
(RHOIPTELEACEAE, JUGLANDACEAE)

Though pollen of the monotypic Rhoipteleaceae exhibits spinulate sculpturing and a relatively thick, narrowly channeled tectum similar to that of *Ticodendron*, other pollen characters differ significantly. Pollen of Rhoipteleaceae is tricolporate, the spinules are solitary, shorter than those in *Ticodendron*, and tend more toward scabrae than spinules. The narrow interstitium, composed of extremely thin, sparsely distributed columellae and sporadic small granules, is supported by a thick, continuous foot layer and endexine continuous around the grain with significant thickening at the aperture (Stone & Broome, 1971).

Like *Ticodendron*, pollen of Juglandaceae is por-

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FIGURES 1–5. *Ticodendron incognitum* (cryo-SEM, SEM).—1. Polar view (SEM); ×2,950.—2. Equatorial view including one of the small aspidote pores (SEM); ×2,860.—3. Detail of exine surface. Acute-tipped spinules are confined to rugulate ridges separated by sparsely microperforate exine (SEM); ×12,000.—4. Cryosection through the interior of the aspidote apertural region revealing disorganized disrupted exine surrounding the pore (cryo-SEM); ×9,900.—5. Cryosection through nonapertural exine composed of numerous, typically pendent, irregularly shaped, occasionally laterally fused columellae and sparse granules (cryo-SEM); ×25,000. Bar in each micrograph equals 1 μm.

ate and spinulate with an exine characterized by a narrowly channeled tectum and low to moderately protruding aspidote apertures composed only of tectum and granular, spongy interstitial elements. However, there are also significant differences from *Ticodendron*. Pore number among Juglandaceae is highly variable (range 2–20 pores) and, in several genera, the pores are nonuniformly distributed over the surface. The spinules are solitary and evenly spaced. The interstitium is predominantly finely granulate with the granules randomly anastomosing to form a spongy network in contrast to the isolated granules found among the other families. Columellae are sporadic, extremely thin, and typically fused only with the tectum. In several taxa, the interstitial elements are suspended from the tectum and separated from the foot layer by a broad exine-free zone resulting from the outward curvature of the tectum (Stone & Broome, 1975).

CASUARINALES (CASUARINACEAE)

Pollen of Casuarinaceae and *Ticodendron* exhibit a significant number of pollen similarities. Pollen in both taxa is triporate with slightly to moderately protruding aspidote pores. Exine sculpture is minutely spinulate with the spinules arranged in single file confined to rugately arranged short ridges. The exine is characterized by a thick, evenly thickened tectum with narrow radial channels and perforations and a wide interstitium composed of broad, prominent columellae supported by a thick foot layer. The columellae typically extend up to, but do not fuse with, the foot layer. The apertural exine is composed only of pendent columellae and granules with the foot layer terminating approximately 2–3 μm back from the pore.

Pollen differences between Casuarinaceae and *Ticodendron* include more protruding aspidote pores and a more prominently rugulate exine in Casuarinaceae. Ultrastructurally, endexine is absent in *Ticodendron* and the columellae are (1) more irregular in shape; (2) often associated with granular elements; (3) frequently pendent from the tectum extending only half the width of the nonapertural interstitium; and (4) occasionally laterally fused in localized regions just below the tectum.

MYRICALES (MYRICACEAE)

Pollen of Myricaceae (only *Myrica* examined) is strikingly similar to that of *Ticodendron*. *Myrica* pollen is triporate with aspidote apertures, spinulate with thinner exine in equatorial than polar regions, and a wholly ektexinous exine organized into a thick, evenly thickened tectum with narrow, radial channels and perforations, a prominent interstitium often equal in thickness to the tectum, and a thick continuous foot layer. Apertures are similarly composed of only imperforate tectum and pendent, slightly larger columellae and granules, the latter tending to cluster along the lower surface of the interstitium (Coetzee & Praglowski, 1984).

Differences between *Myrica* and *Ticodendron* center on pore and sculpturing characters and elements of the interstitium. Pores of *Myrica* are consistently prominently aspidote as opposed to low-lying to moderately protruding in *Ticodendron*. Though *Myrica* and *Ticodendron* exhibit spinulate sculpturing, each spinule in the former is restricted to a small elevation, which usually anastomoses with other spinule elevations to form irregularly shaped islands. Interstitial elements in *Myrica* are predominantly large, ovoid coarse granules, which extend the entire width of the interstitium but do not fuse with the tectum or foot layer. The overall morphology of the myricaceous interstitial element, despite its granular nature, approaches that of the nonapertural pendent columellae of *Ticodendron*.

FAGALES (ONLY BETULACEAE)

In contrast to the Fagaceae, the Betulaceae, particularly *Carpinus* and *Ostrya*, exhibit several pollen characters similar to those of *Ticodendron*.

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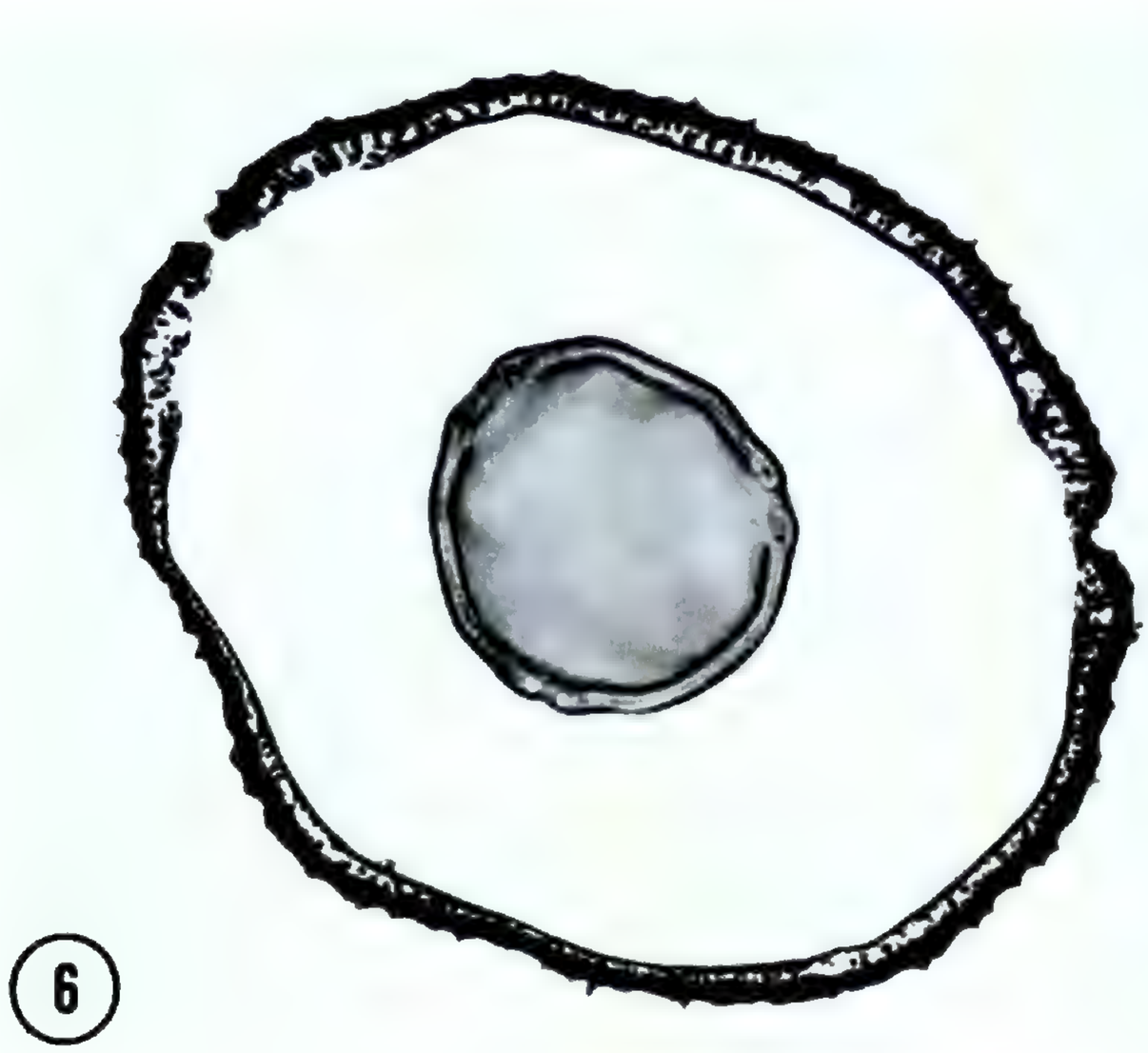
FIGURES 6–11. *Ticodendron incognitum* (LM, TEM).—6. Equatorial section through two apertures (TEM); ×3,400. Inset: Equatorial view including three slightly subequatorial pores (LM); ×950.—7. Detail of nonapertural exine. The columellae are typically pendent from the tectum, broad, irregularly shaped and rarely connected to the foot layer (TEM); ×18,000.—8. Nonapertural exine composed of thick, channeled tectum, columellate/granulate interstitium and continuous irregularly thickened foot layer; ×8,600.—9. Detail of exine sectioned directly through the pore. Approximately 3 μm back from the pore the foot layer thickens slightly, becomes lamellate then terminates abruptly (arrow). Approaching the pore opening, the columellae elongate and granules become more numerous. Thin, finely granular exine (arrowhead) surrounds the pore opening (TEM); ×12,000.—10. Section through apertural region peripheral to the pore opening. The exine is organized into dense, loosely attached, irregularly shaped segments and granules (TEM); ×7,000.—11. Equatorial exine adjacent to pores. This region of exine is characterized by an interstitium significantly reduced in thickness compared to that seen in other nonapertural regions (TEM); ×14,200. Bar in each micrograph equals 1 μm.



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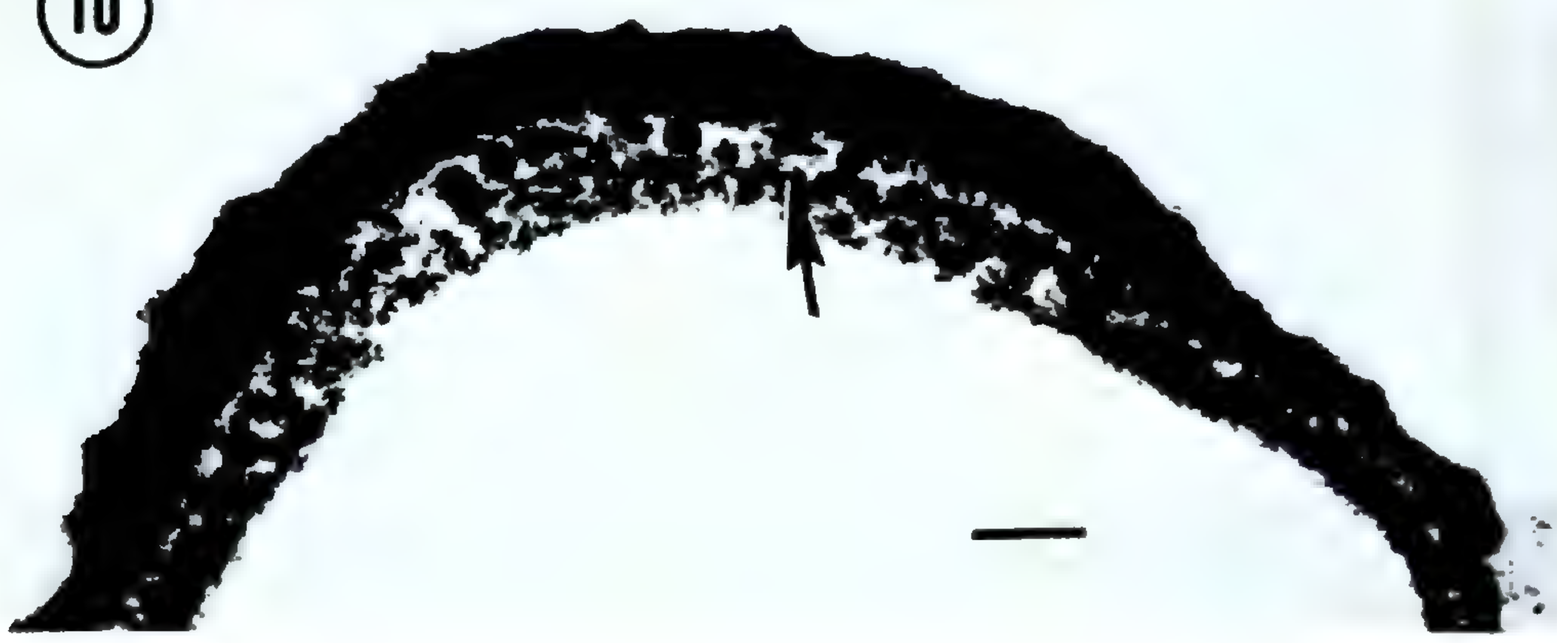

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Betulaceae pollen is characterized by three low-lying to moderately projecting aspidote pores. Sculpturing is strictly spinulate with the spinules typically restricted to short rugulate ridges, which tend to be more prominent in *Alnus* and *Betula*. The tectum in all genera is uniformly thickened and exhibits narrow radial channels and perforations. Pollen of *Carpinus* and *Ostrya* exhibits the greatest overall similarity to *Ticodendron*. In all three taxa the interstitium is columellate to columellate/granulate (though the columellae are extremely small in Betulaceae), the organization of the reduced ektexine in equatorial areas is identical, endexine is absent and the apertural exine is composed simply of granular and, more rarely, columellar elements pendent from the tectum with the foot layer ceasing several micra back from the pore opening (Feuer & Crane, 1984; Feuer, unpublished data).

Differences between Betulaceae and *Ticodendron* center on characters of the interstitium, foot layer, and organization of the aperture. In Betulaceae: (1) the interstitium in unreduced areas is narrower, often ½ the thickness of the tectum compared to an interstitium equal to or slightly greater in thickness than the tectum in *Ticodendron*; (2) the foot layer, except in *Alnus* and *Ostryopsis*, is evenly thickened with smooth upper and lower surfaces; and (3) *Betula*, *Alnus*, and *Corylus* exhibit vestibulate apertures associated with prominent endexine.

Systematic Relationships of *Ticodendron*

In assessing the relationships of *Ticodendron*, characters of exine sculpturing were used to establish the initial link between *Ticodendron* and the "higher" Hamamelidae. Excluding Fagaceae, most of these families have predominantly spinulate pollen. Pollen aperture type and shape (ratio of polar to equatorial axes) were also considered of prime importance since they are usually more evolutionarily conservative, particularly at the familial level, than other pollen features. Similarities in ultrastructural elements of the exine were ranked next in diagnostic value. These included, in order of importance, the occurrence of an evenly thickened tectum with extremely narrow, radial channels and perforations, the presence or absence of endexine, the organization of the apertural exine, the nature of the interstitial elements, the width of the interstitium, and the thickness and continuity of the foot layer.

The pollen data offer strong support for placement of *Ticodendron* among the "higher" Hamamelidae (Casuarinales, Fagales, Myricales, Juglandales) as suggested by Tobe (1991) and Hickey (1991), and not the Dilleniidae as proposed by Wolfe (1989). Wolfe also maintained that *Ticodendron* must exhibit the compound aperture and other specialized features of the fossil Normapolles-type pollen in order to be considered a member of the Hamamelidae rather than the Dilleniidae (pers. comm.).

Evidence for a link between Normapolles and *Ticodendron* is not a requisite for considering *Ticodendron* to be a "higher" hamamelid. Taxonomically, Normapolles genera are in a confused state because of the considerable morphological variation among the 100 or so currently recognized forms. Evolutionary relationships based on these highly variable forms would be tenuous at best. Though some Normapolles pollen types have been shown to be juglandalean by their association with macrofossils (Friis, 1983), the majority remain as form genera without established evolutionary relationships. Some of the more atypical forms may even be of nonhamamelid origin (Batten, 1989).

Ticodendron, with its triporate aspidote apertures, minutely spinulate exine, tectum with narrow radial channels, prominent columellate/granulate interstitium, continuous foot layer, and apertures composed only of tectum and pendent interstitial elements belongs among the hamamelids with its closest relationships near Casuarinales and Myricales. Pollen data suggest little or no link to the Fagales and Juglandales. Though Urticalean pollen appears significantly different from that of *Ticodendron*, the pollen data are too incomplete to allow for adequate comparison and analysis.

Pollen of Casuarinales and *Ticodendron* exhibit moderately protruding aspidote pores, suboblate to oblate shapes, spinules confined to short, rugately arranged ridges, and a wide interstitium composed mainly of prominent columellae, which typically are not fused to the foot layer. Aperture structure is identical in Casuarinales and *Ticodendron*. Casuarinales can only really be distinguished palynologically from *Ticodendron* at the ultrastructural level by its longer columellae, which typically extend the entire width of the interstitium, the absence of nonapertural interstitial granules, and the presence of endexine. The occurrence of endexine in Casuarinales may not be as significant a difference as it at first appears since the endexine is extremely thin and occurs only in nonapertural areas.

Pollen similarities between Myricales and *Ticodendron* include suboblate shape, the presence

of coarse columella-like granules in a wide interstitium, the occurrence of a thick, continuous foot layer, and the absence of endexine. Like the Casuarinales, Myricales and *Ticodendron* exhibit an identical aperture structure including the presence of clustered granules in basal regions of the aperture (Fig. 10, arrow). Pollen of Myricales can be distinguished from that of *Ticodendron* by its more protruding aspidote pores, isolated spinules tending to cluster on small islands of exine, and large, coarse, granular elements, which approach columellae in overall morphology but are not fused to the tectum or the foot layer.

The Juglandales, with their tricolporate (Rhoipteleaceae) and 2–20-porate (Juglandaceae) pollen, uniformly distributed, solitary, spinulate sculpturing and spongy, granular, interstitium composed of a randomly anastomosing network of fine granules, are remote from *Ticodendron*.

Connections to the Fagales are even more remote than those of the Juglandales. Pollen of Balanopaceae and Fagaceae, including the distinctive *Nothofagus*, differs in every fundamental aspect from that of *Ticodendron*. Only Betulaceae could be considered as possibly linked to *Ticodendron*. A relationship in Betulaceae would have to lie with the simple aperturate, endexine-free pollen of *Carpinus* and/or *Ostrya*. *Alnus*, with its multiaperturate, arcuate pollen exhibiting a spongy, granular interstitium and compound apertures, is far removed from *Ticodendron* as is *Betula* with its multiporate, similarly compound vestibulate apertures characterized by well-developed endexine.

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NEW SPECIES OF *PANICUM* SUBGENUS *DICHANTHELIUM* (POACEAE: PANICEAE) FROM SOUTH AMERICA

Fernando Zuloaga[1] *and Osvaldo Morrone*[1]

ABSTRACT

Six new species of the pantropical genus *Panicum* subg. *Dichanthelium* (Poaceae: Paniceae) are described, illustrated, and compared with the putative most closely related species. Five of these species, *P. heliophilum*, *P. adenorhachis*, *P. cabrerae*, *P. petropolitanum*, and *P. cucaense*, are found in campos rupestres, which are high-altitude rocky fields of Brazil. *Panicum davidsei* is restricted to elevated savannas of Venezuela and northwestern Brazil.

During the revision of *Panicum* for America by the senior author, six new species were discovered in South America, all of which belong in subg. *Dichanthelium* A. Hitchc. & Chase.

Subgenus *Dichanthelium* was traditionally characterized (Hitchcock & Chase, 1910, 1915; Pilger, 1940; Hsu, 1965) as having two vegetative phases: one with a rosette of short, broad leaves formed during autumn and winter that produce primary panicles with chasmogamous spikelets on elongated shoots in spring; and the other with fascicles of short branches that produce secondary panicles with cleistogamous spikelets during spring, summer, and autumn.

Gould (1974) recognized *Dichanthelium* at the generic level, an idea followed by a number of different authors (e.g., Brown & Smith, 1975; Clark & Gould, 1975; Gould & Clark, 1978; Gould, 1980; Hansen & Wunderlin, 1988).

Pohl (1980) and Zuloaga (1987) reported variation in the vegetative characters among Central and South American species of *Dichanthelium*. Lelong (1984), Zuloaga (1987), and Webster (1988) recognized *Dichanthelium* as a subgenus of *Panicum*. Due to the absence of rosette and chasmogamous and cleistogamous panicles on the Central and South American species of the subgenus, it can be recognized by having inflorescences lax and diffuse, spikelets ellipsoid to obovoid, with the upper anthecium indurate, smooth, with simple papillae on its surface, and apiculate, the apicule covered with stomata and with or without unicellular macrohairs. The leaf anatomy is uniform in the subgenus and is non-Kranz, with two bundle sheaths around the vascular bundles, the mesophyll irregularly radiate around the vascular bundles, and with extensions of the parenchymatous sheath present toward both surfaces of the blade.

Within subg. *Dichanthelium*, the new species are placed in sect. *Dichanthelium* because of their membranous-ciliate ligules, spikelets with the upper glume and lower lemma 7–9(–14)-nerved, the upper anthecium apiculate and papillate, with simple papillae regularly distributed, and the upper lemma apically pilose or scabrous.

Five of these species are found in Brazil, in campos rupestres, rocky fields at moderate altitudes 1,000–1,800 m (Eiten, 1978), or in rocky mountains of higher altitudes (over 2,000 m) near Rio de Janeiro. The other species grows in elevated savannas in Venezuela and northwestern Brazil.

Panicum heliophilum Chase ex Zuloaga & Morrone, sp. nov. TYPE: Brazil. Minas Gerais: Chapeo de Sol, Serra do Cipó, 110 km NE of Belo Horizonte, 900 m, 28 Mar.–1 Apr. 1925, *A. Chase 9147* (holotype, US; isotypes, F, GH, MO). Figure 1.

Panicum pycnoclados Tutin affine sed spiculis hirsutis sine stipite, et foliis rigidis, lineari-lanceolatis, basi subcordatis differt.

Plants perennial, short-rhizomatous. Culms 50–70(–100) cm tall, many-noded, tangled, leaning on the adjacent vegetation, the basal portion decumbent and geniculate, the upper portion erect, freely branching; internodes cylindric, pilose, solid toward the base, otherwise hollow; nodes villous. Sheaths striate, 0.5–4 cm long, strongly distichous,

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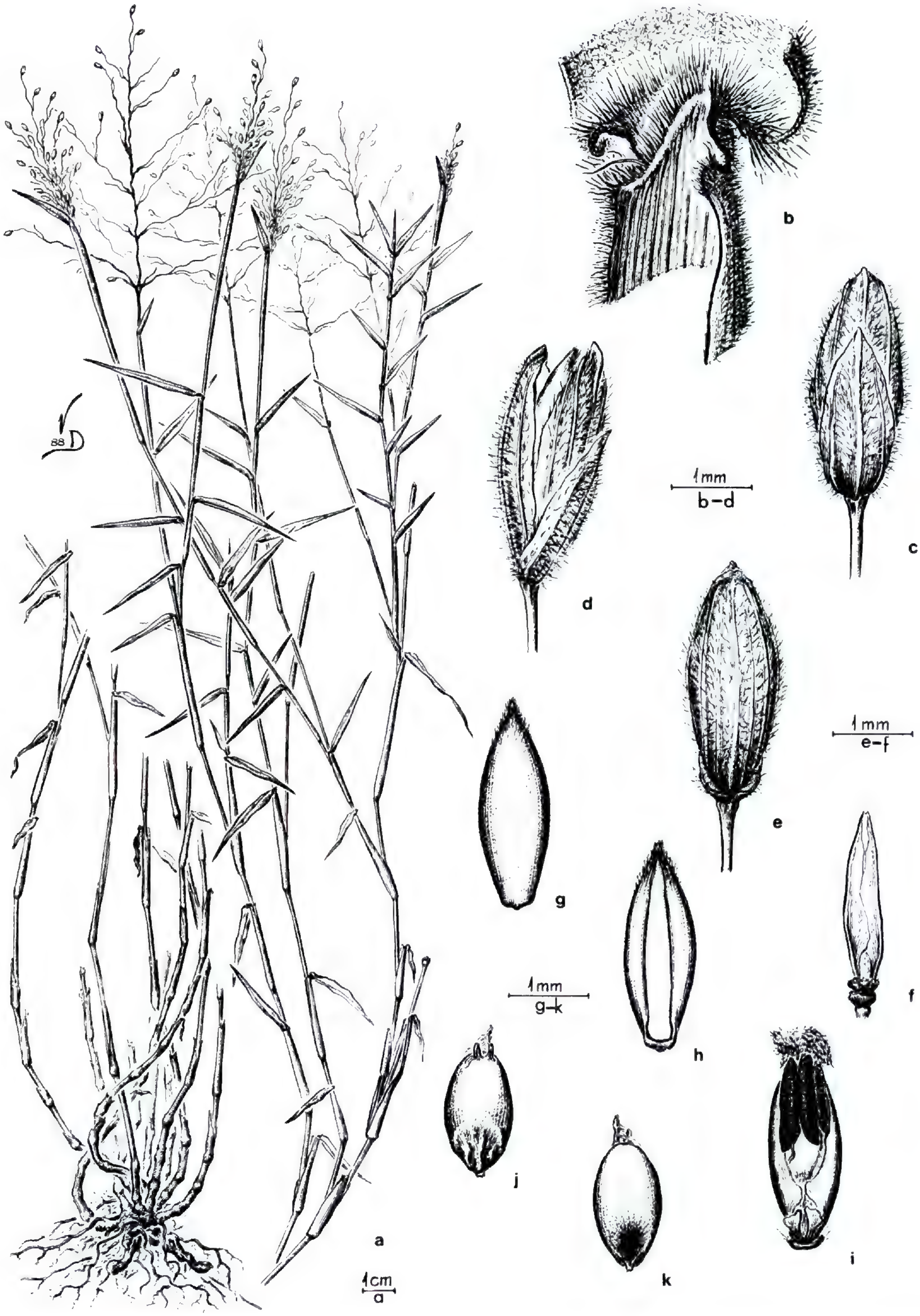

FIGURE 1. Holotype of *Panicum heliophilum*.—a. Habit.—b. Ligule.—c. Spikelet, ventral view.—d. Spikelet, lateral view.—e. Spikelet, dorsal view.—f. Lower palea.—g. Upper anthecium, dorsal view.—h. Upper anthecium, ventral view.—i. Upper palea with lodicules, stamens, and stigmas.—j. Caryopsis, embryo side.—k. Caryopsis, hilum side.

hispid with short hairs, the margins long-ciliate; auricles small, pilose; collar brownish to purplish, covered with short, whitish hairs; ligule a ciliate membrane, 0.2–0.7 mm long, the cilia 0.1–0.6 mm long; blades linear-lanceolate, 4–5(–12) cm long, 0.3(–1) cm wide, subcordate, densely hirsute on both surfaces, flat or folded, the margins cartilaginous, scabrous, and short-ciliate. Primary panicles lax, diffuse, 4–16 cm long, 3–13 cm wide; peduncles hispid, up to 8 cm long; branches opposite or alternate, the lower ones sometimes whorled, diverging from the axis; rachis flexuous, sparsely hirsute, the axes of the branches short-hirsute or glabrous, the axils of the branches brownish, hispid; pedicels smooth, glabrous, 2–13 mm long. Secondary panicles similar to the terminal one, smaller. Spikelets solitary, ellipsoid, 2.6–3.1 mm long, 1–1.1 mm wide, hirsute, greenish, without a stipe between the lower and upper glume; lower glume 2–2.7 mm long, ¾ the length of the spikelet, acuminate, 3-nerved, the nerves anastomosed toward the distal portion; upper glume and lower lemma subequal, 7-nerved; lower palea elliptic, 2 mm long, 0.3 mm wide, hyaline; lower flower absent; upper anthecium long-ellipsoid, 2.4–2.7 mm long, 0.8–0.9 mm wide, stramineous, brownish at maturity, papillose, with simple papillae evenly distributed, densely pilose, with appressed, long hairs toward the apex of lemma and palea; upper lemma 5–7-nerved; rachilla prolonged or not into a short mucro above the upper anthecium; lodicules 2, fleshy, conduplicate, truncate, ca. 0.6 mm long; stamens 3, the anthers ca. 1.3 mm long, purplish; stigmas plumose. Caryopsis ellipsoid, 1.4 mm long, 0.8 mm wide, brownish; hilum oblong; embryo ⅓ the length of the caryopsis.

Paratypes. BRAZIL. MINAS GERAIS: Diamantina, summit of Serra de San Antonio, 1,400 m, 27–30 Dec. 1929, *A. Chase 10354* (US); Mun. Jaboticatubas, Lagoa Santa a Conceição do Mato Dentro, 27 July 1977, *Sendulsky & Burman 1920* (SI, SP); km 114 ao largo da rodovía Lagoa Santa–Conceição do Mato Dentro, 1,160 m, *Sendulsky 1609* (SP); Serra de Santo Antonio, 2–5 km ao leste da cidade de Diamantina, 1,050–1,100 m, 10 Feb. 1982, *Burman & Sendulsky 696, 697, 709* (SI, SP); Serra do Cipó, ao longo da rodovía Lagoa Santa–Conceição, 9 Dec. 1971, *Sendulsky 446* (SP); Serra do Cipó, 25 Feb. 1979, *Burman 525* (SP), 24 June 1979, *Burman 485* (SP).

Panicum heliophilum is most closely related to *P. pycnoclados* Tutin, from which it differs by having hirsute, nonstipitate spikelets and stiff, linear-lanceolate blades with subcordate bases. *Panicum pycnoclados* has glabrous to sparsely hispid spikelets and lax, lanceolate to ovate-lanceolate blades that are cordate and amplexicaulous.

Panicum heliophilum is also related to *P. assurgens* Renvoize; it differs by having leaf blades linear-lanceolate, rigid, usually folded and densely hirsute, and spikelets hirsute 2.6–3.1 mm long. *Panicum assurgens* has leaf blades lanceolate, flat, herbaceous, sparsely hispid, and spikelets puberulous to glabrous, 3.3 mm long.

Some of the specimens examined have the rachilla prolonged above the upper anthecium as a short mucro, a character also present in other genera of Paniceae [*Lasiacis grisebachii* (Nash) A. Hitchc. and *L. ruscifolia* (HBK) A. Hitchc. (Davidse, 1978); *Brachiaria tatianae* Zuloaga & Soderstrom (Zuloaga & Soderstrom, 1985)].

In *Panicum heliophilum* the lower leaf blades abscise, leaving the dry leaf sheaths on the culms. This is probably an adaptation to the seasonally dry habitat. It also occurs in *P. adenorhachis*. *P. cabrerae*, and *P. cucaense*, species that grow in a similar habitat.

Panicum heliophilum grows in campos rupestres of the state of Minas Gerais, Brazil, between 900 and 1,400 m elevation. It is common in sandy soils, where it is found, according to notes on *Chase 9147*, "in dry rocks, leaning out, tangled with *Echinolaena inflexa* and resembling it."

Panicum adenorhachis Zuloaga & Morrone, sp. nov. TYPE: Brazil. Bahia: Mun. Rio de Contas, 6–10 km ao NW de Rio de Contas, na estrada para o Pico das Almas, 13°32′S, 41°53′W, 1,000 m, 21 July 1979, *S. A. Mori, R. M. King, T. S. dos Santos & J. L. Hage 12451a* (holotype, CEPEC; isotypes, MO, US). Figure 2.

Panicum stipiflorum Renvoize affine sed foliis lanceolatis, glandulosis et spiculis 2.7–3 mm longis sine stipite, gluma inferiore quam spicula ⅓ vel minus longiore, enervia vel uninervia differt.

Plants perennial. Culms trailing, leaning over the adjacent vegetation, many-noded, sparingly branched; internodes cylindric, hollow, glabrous; nodes brownish, short-pilose or glabrous. Sheaths striate, caducous, glabrous, covered with small glands, the margins long-ciliate; collar short-pilose, ligule a ciliate membrane, 0.2–0.6 mm long; blades narrowly lanceolate, flat, 4–6 cm long, 0.3–0.5 cm wide, subcordate, the adaxial surface scabrous, the abaxial surface glabrous and covered with small glands, the basal margins long-ciliate with tuberculate hairs but otherwise scabrous. Primary panicles lax, diffuse, few-flowered, 5–7 cm long, 4–5 cm wide; rachis wavy and glandular, the nodes distant; branches widely divergent, solitary at each

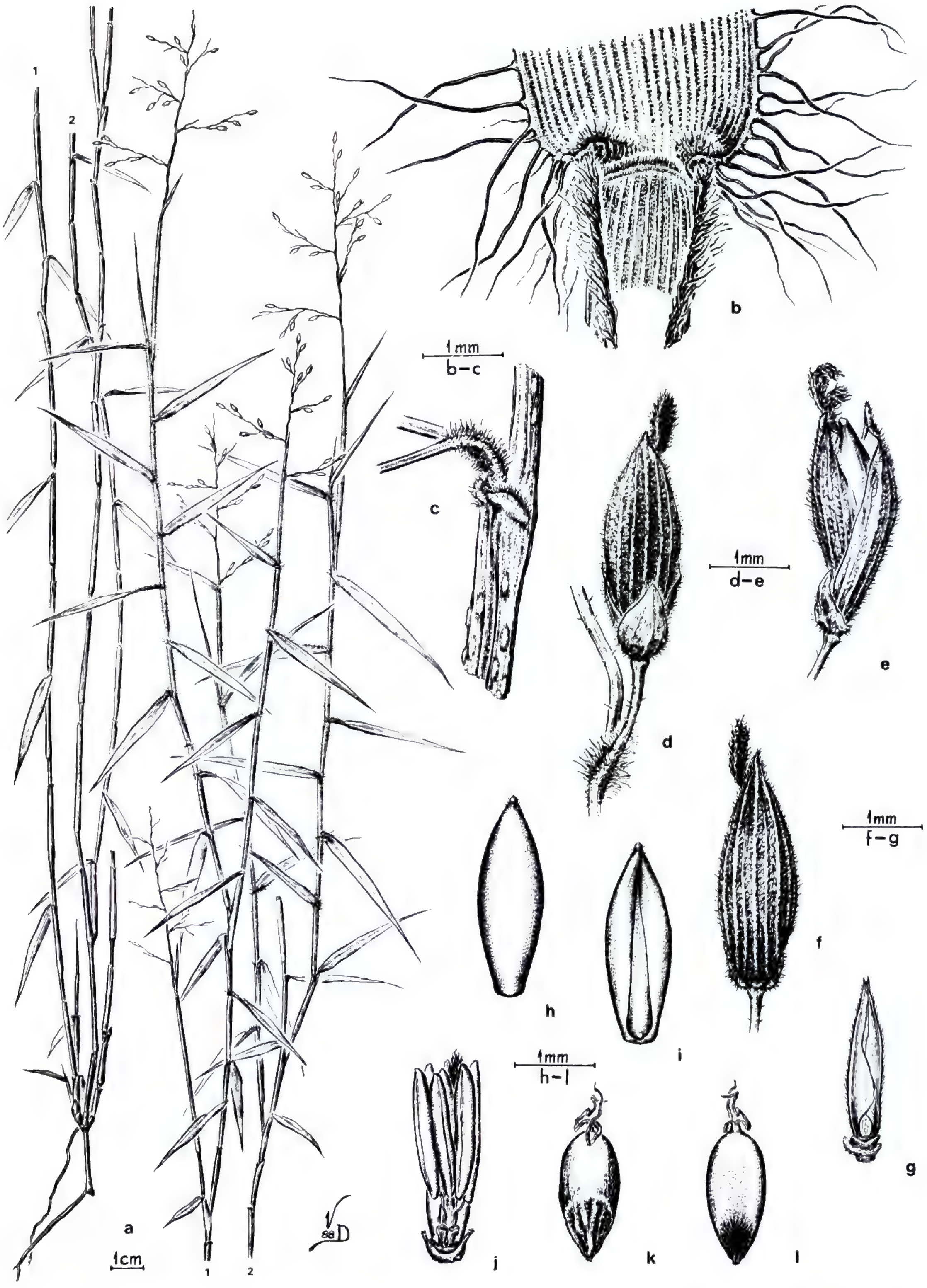

FIGURE 2. Holotype of *Panicum adenorhachis*.—a. Habit.—b. Ligule.—c. Axis of the panicle with glands.—d. Pedicel and spikelet, ventral view.—e. Spikelet, lateral view.—f. Spikelet, dorsal view.—g. Lower palea.—h. Upper anthecium, dorsal view.—i. Upper anthecium, ventral view.—j. Upper palea with lodicules and stamens.—k. Caryopsis, embryo side.—l. Caryopsis, hilum side.

node with scabrous and glandular axes and long-pilose axils; pedicels claviform, short pilose. Secondary panicles similar to the terminal one. Spikelets solitary and widely spaced, long-ellipsoid, 2.7–3 mm long, 0.9 mm wide; lower glume 0.7–0.8 mm long, less than ⅓ the length of the spikelet, acuminate, enervate to 1-nerved, hyaline; upper glume and lower lemma 9-nerved, short-hispid, subequal, longer or shorter than the upper anthecium; stipe lacking between the lower and upper glume; lower palea lanceolate, 1.8 mm long, 0.4 mm wide, hyaline, ciliolate on the margins; lower flower absent; upper anthecium long-ellipsoid, 2.3 mm long, 0.8 mm wide, stramineous, brownish at maturity, papillose with simple papillae in longitudinal rows; upper lemma short-mucronate and with small macrohairs at the apex; rachilla prolonged beyond the upper anthecium as a short mucro; lodicules 2, conduplicate, truncate, ca. 0.3 mm long; stamens 3, the anthers 1.5 mm long; stigmas plumose. Caryopsis ellipsoid, brownish, 1.5 mm long, 0.7 mm wide; hilum punctiform; embryo less than ½ the length of the caryopsis.

Paratype. BRAZIL. BAHIA: Alto do Pico das Almas, 1,850 m, 20 Feb. 1987, *Harley et al. 24460* (K).

Renvoize (1984) treated the collection *Mori et al. 12451a* as *P. stipiflorum* Renvoize. *Panicum adenorhachis* differs from *P. stipiflorum* by having lanceloate blades that are attenuate at the base, scabrous adaxially, and glandular abaxially; nonstipitate spikelets 2.7–3 mm long; enervate or 1-nerved lower glume that is less than ⅓ the length of the spikelet; and the evidently glandular rachises of the panicles.

Panicum stipiflorum has leaf blades ovate-lanceolate, cordate and amplexicaul, densely to sparsely hirsute on both surfaces, without glands; spikelets 2–2.6 mm long, with a manifest stipe between the lower and upper glume, lower glume 3–5-nerved, ½ (occasionally ⅔) the length of the spikelet, and rachis of the inflorescence without glands.

Panicum cumbucana Renvoize differs from *P. adenorhachis* by having nonglandular, short (1–2 cm), and narrow (0.3–0.6 cm) blades that are cordate at the base; nonglandular rachises; stipitate spikelets 1.9–2.4 mm long; and lower glumes (1–)3-nerved, ½ the length of the spikelet.

Panicum adenorhachis has glands on the leaf blades and panicles, a feature also present in other species of subg. *Dichanthelium*, e.g., *P. sabulorum* Lam., *P. stigmosum* Trin., *P. strigosum* Muhl., and *P. sphaerocarpon* Elliott.

Panicum adenorhachis inhabits campos rupestres of the state of Bahia, Brazil.

Panicum cabrerae Zuloaga & Morrone, sp. nov. TYPE: Brazil. Bahia: Mun. Rio de Contas, Pico das Almas, a 18 km ao SNW de Rio de Contas, 13°33′S, 41°57′W, 1,600–1,850 m, 22 July 1979, *S. A. Mori, R. M. King, T. S. dos Santos & J. L. Hage 12475* (holotype, CEPEC; isotypes, MO, US). Figure 3.

Panicum stipiflorum Renvoize affine sed reclinatum, foliis lineari-lanceolatis, basi attenuatis, longe pilosis sine marginibus ciliatis differt.

Plants perennial. Culms ca. 50 cm tall, leaning over the vegetation, many-noded, sparingly branched; internodes cylindric, hollow, sparsely pilose with whitish hairs; nodes densely pilose with long, whitish hairs. Sheaths striate, 1.5–2 cm long, longer than the internodes, long-hispid, the margins pilose with whitish hairs, especially toward the upper portion; auricles small, pilose; collar pilose; ligule a ciliate membrane, ca. 0.2 mm long; blades linear-lanceolate, 4–6 cm long, 0.2 cm wide, basally attenuate, apically acuminate, densely pilose, with long, whitish hairs on both surfaces, caducous at maturity, the margins involute. Panicles lax, diffuse, 4.5–6 cm long, 3.5–6 cm wide; peduncles hispid, 5–7 cm long; rachis cylindric, densely hispid on the lower portion, otherwise glabrous, the nodes distant; branches alternate, divergent and reflexed, basally hispid, distally glabrous, the axils pilose to glabrous; pedicels claviform, smooth, glabrous, 2–9 mm long. Spikelets solitary, ellipsoid, 2–2.3 mm long, 0.8–0.9 mm wide, plano-convex, hirsute with whitish hairs on the glumes and lower lemma; lower glume 1.1–1.3 mm long, nearly ½ the length of the spikelet, 3-nerved, acute, a small stipe present between the lower and upper glume; upper glume 9-nerved, the nerves anastomosing toward the apex; lower lemma 9-nerved; lower palea lanceolate, 1.5–1.8 mm long, 0.3 mm wide, glabrous, truncate, hyaline; lower flower absent; upper anthecium ellipsoid, 1.9 mm long, 0.7 mm wide, papillose, with simple papillae all over its surface, glabrous or with a few microhairs toward the apiculate apex; rachilla prolonged or not beyond the upper anthecium as a short mucro; lodicules 2, truncate, ca. 0.2 mm long; stamens 3, the anthers 1.2 mm long; stigmas plumose. Caryopsis obovoid, 1.1 mm long; hilum oblong; embryo less than ⅓ the length of the caryopsis.

Panicum cabrerae is related to *P. stipiflorum*, *P. adenorhachis*, and *P. congestum* Renvoize. *Panicum stipiflorum* has ovate-lanceolate, cordate, glabrous to short-pilose blades with ciliate margins, upper anthecium pilose at apex, and culms decumbent and prostrate at the base, then becom-

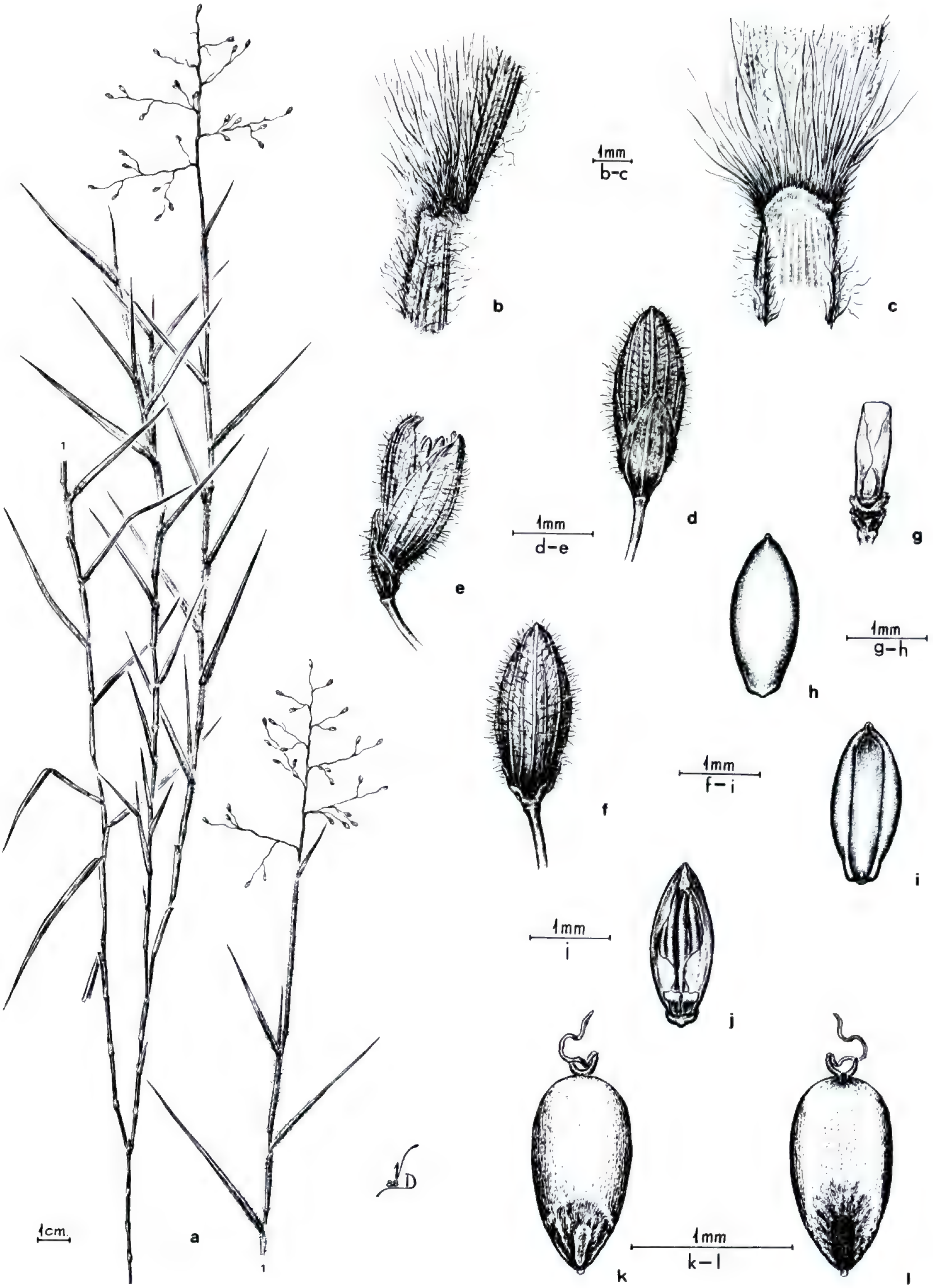

FIGURE 3. Holotype of *Panicum cabrerae*. —a. Habit.—b. Sheath and lower portion of a leaf blade.—c. Ligule.—d. Spikelet, ventral view.—e. Spikelet, lateral view.—f. Spikelet, dorsal view.—g. Lower palea.—h. Upper anthecium, dorsal view.—i. Upper anthecium, ventral view.—j. Upper palea with lodicules and stamens.—k. Caryopsis, embryo side.—l. Caryopsis, hilum side.

ing erect. *Panicum adenorhachis* has, in relation to *P. cabrerae*, bigger, short-hispid spikelets, glands on the leaf blades and panicles, a lower glume less than ⅓ the length of the spikelet, and spikelets nonstipitate between the lower and upper glume. *Panicum congestum* differs from *P. cabrerae*, *P. stipiflorum*, and *P. adenorhachis* by having spikelets 2.8–3.2 mm long, with a lower glume ¾ the length of the spikelet, panicles partially included in the leaf sheaths and few-flowered, with only two or three spikelets per panicle.

The holotype of *P. cabrerae*, *Mori et al. 12475* (CEPEC), was treated as *P. stipiflorum* by Renvoize (1984).

Panicum cabrerae grows in a habitat similar to that of *P. adenorhachis*.

We name this species in honor of Angel L. Cabrera, major professor of the senior author, who is especially grateful for the training in systematics provided by Prof. Cabrera.

Panicum davidsei Zuloaga & Morrone, sp. nov. TYPE: Venezuela. Bolívar: Cabanayén, La Gran Sabana, wet inundated savanna, 1,300 m, 3 Dec. 1973, *G. Davidse, M. Ramia & R. Montes 4796* (holotype, MO). Figure 4.

Panicum assurgens Renvoize affine sed spiculis stipitatis, gluma superiore 12–14-nervia et lemma inferiore 10–12-nervia; lemma superiore conspicue apiculata cum marginibus superioribus membranaceis differt.

Plants perennial. Culms 0.50–1.80 m long, decumbent, rooting and branching at the lower nodes, the upper portions erect; internodes 8–22 cm long, cylindric, striate, hispid, compressed; nodes hirsute. Sheaths 5–8 cm long, sparsely hirsute with long tuberculate hairs, one of the margins long-ciliate, the other membranous; collar long-pilose with whitish hairs; ligule membranous-ciliate, ca. 0.2 mm long; blades narrowly lanceolate, 9–13 cm long, 1–1.3 cm wide, flat, subcordate, the apex acuminate, adaxial surfaces long-pilose toward the base, otherwise glabrous, abaxial surfaces sparsely pilose, the margins scabrous and ciliate toward the base, the midnerve conspicuous. Panicles lax, diffuse, 12–20 cm long, 7–12 cm wide; peduncle 10–40 cm long; rachis cylindric, striate, pilose near the branches, otherwise glabrous; lower branches whorled, the upper ones subopposite or alternate, the axes of the branches flexuous, glabrous, the axils of the branches pilose; pedicels glabrous, wavy. Spikelets solitary, ellipsoid, 3–3.3 mm long, 1 mm wide, scaberulous, attenuate toward the base and with a small stipe between the lower and upper glume; lower glume ovate-acuminate, 1.5–1.8 mm long, nearly ½ the length of the spikelet, 3-nerved; upper glume 2.4–2.7 mm long, not covering the apex of the upper anthecium, 11–14-nerved; upper glume and lower lemma subequal with manifest nerves anastomosed toward the apex; lower lemma ca. 2.7 mm long, 10–12-nerved; lower palea lanceolate, 2.1–2.4 mm long, 0.3 mm wide, glabrous, hyaline; lower flower absent; upper anthecium ellipsoid, 2.4–2.7 mm long, 1 mm wide, papillose, apiculate; upper lemma with a green, scabrous crest on the apex and the upper margins membranous, prolonged toward the apex as small wings; rachilla prolonged beyond the upper anthecium as a small mucro; lodicules 2, conduplicate, truncate, ca. 0.4 mm long; stamens 3, the anthers ca. 1.2 mm long; stigmas plumose. Caryopsis ellipsoid, 1.8 mm long; 0.9 cm wide; hilum punctiform; embryo ⅓ the length of the caryopsis.

Paratypes. BRAZIL. RORAIMA: aldeia do Tuchana, *Rondón s.n.*, July 1927 (RB 110786). VENEZUELA. BOLÍVAR: entre Piedra de La Virgen y la parte alta de La Escalera, carretera a La Gran Sabana, 6°0′N, 61°25′W, 1,300 m, 12 Ago. 1989, *Zuloaga et al. 4406* (MO, SI, VEN); a 1 km al sur de Puente Sakaika, La Gran Sabana, 1,200 m, 13 Ago. 1989, *Zuloaga et al. 4427* (MO, SI, VEN).

This species is allied to *P. assurgens* Renvoize. *Panicum assurgens* differs from *P. davidsei* by the nonstipitate spikelets, the 9-nerved upper glume and lower lemma, the lower glume ¾–⅘ as long as the spikelet, and the apiculate upper lemma with indurate, not membranous upper margins.

The large number of nerves on the upper glume and lower lemma of this new species suggest a relationship to *P. itatiaiae* Swallen, a Brazilian species described from Rio de Janeiro with spikelets 4.6–4.9 mm long, 1.6–1.7 mm wide. *Panicum davidsei* has spikelets 3–3.3 mm long, 1 mm wide.

Panicum davidsei grows in savannas of the Gran Sabana, Venezuela, and Brazil, Roraima, at the edge of the forests, together with plants of *P. pycnoclados*.

We name this species in honor of its collector, Gerrit Davidse, renowned agrostologist of the Missouri Botanical Garden.

Panicum cucaense Zuloaga & Morrone, sp. nov. TYPE: Brazil. Rio de Janeiro: Mun. Petrópolis, Morro do Cuca, entre Vale dos Videiras e Araras, campo de altitude, 1,600 m, 27 Jan. 1983, *G. Martinelli & E. Simonis 9011* (holotype, RB; isotypes, MO, SI). Figure 5.

Panicum petropolitanum affine sed caespitosum, breviter rhizomatosum, vaginis conspicue distichis, foliis involutis et paniculis breviter pedunculatis differt.

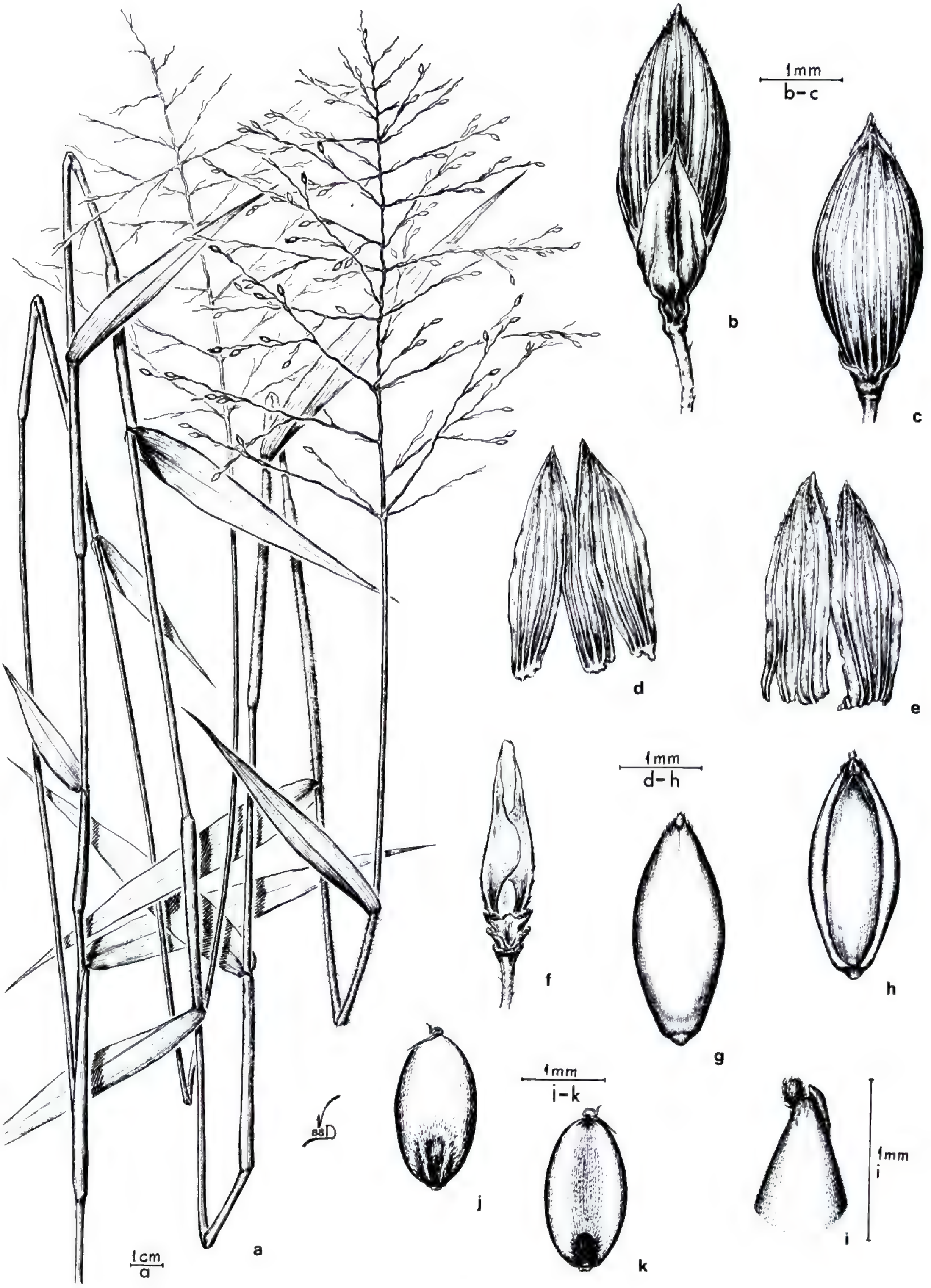

FIGURE 4. Holotype of *Panicum davidsei*.—a. Habit.—b. Spikelet, ventral view.—c. Spikelet, dorsal view.—d. Upper glume.—e. Lower lemma.—f. Lower palea.—g. Upper anthecium, dorsal view.—h. Upper anthecium, ventral view.—i. Upper tip of the lemma with apicule and membranous upper margins.—j. Caryopsis, embryo side.—k. Caryopsis, hilum side.

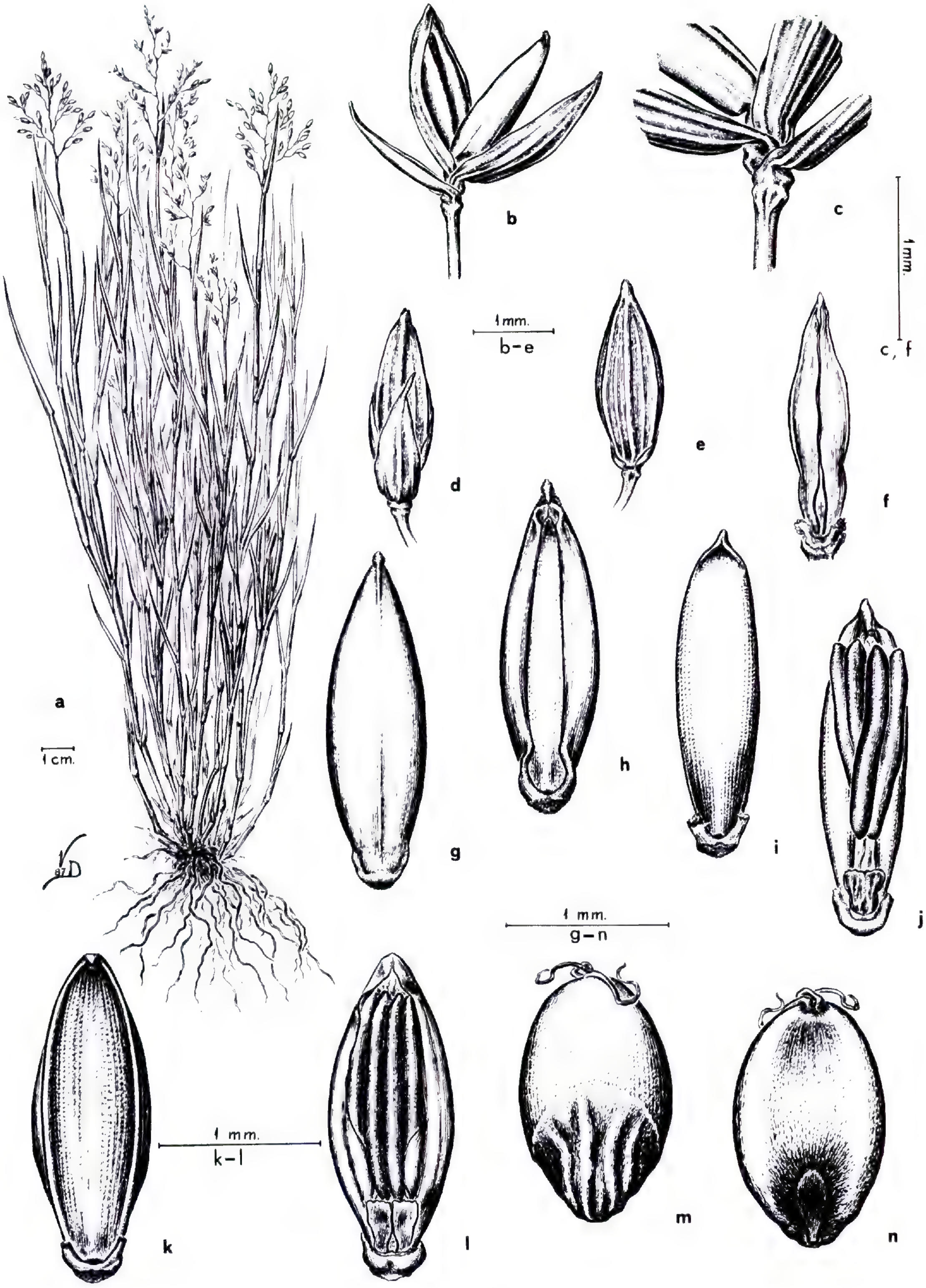

FIGURE 5. Holotype of *Panicum cucaense*. —a. Habit. —b. Spikelet, lateral view. —c. Detail of base of spikelet. —d. Spikelet, ventral view. —e. Spikelet, dorsal view. —f. Lower palea. —g. Upper anthecium, dorsal view. —h. Upper anthecium, ventral view. —i. Upper palea. —j. Upper palea with lodicules and anthers. —k. Upper palea. —l. Upper palea with lodicules and anthers. —m. Caryopsis, embryo side. —n. Caryopsis, hilum side.

Cespitose perennial, shortly rhizomatous. Culms 20–30 cm tall, many-noded, erect to geniculate-ascending and rooting at the lower nodes, freely branching; internodes 1–4 cm long, cylindric, striate, glabrous; nodes compressed, glabrous, brownish. Sheaths striate, ca. 1.2 cm long, longer than the internodes, strongly distichous, long-pilose at the distal portion, otherwise glabrous, one margin pilose with long, whitish hairs, the other membranous; ligule a ciliate membrane, the membrane ca. 0.1 mm long, the cilia 0.4 mm long; blades linear, 1.5–5.5 cm long, 0.1–0.2 cm wide, folded, attenuate toward the apex, pilose adaxially toward the ligule, otherwise glabrous, the borders scabrous. Primary panicles lax, diffuse, few-flowered, 2–3.5 cm long, 1.5–3.5 cm wide; peduncles to 6 cm long, glabrous; rachis striate, wavy, glabrous, with some glands; branches alternate, divergent and widely spaced, glabrous, the axils of the branches pilose; pedicels glabrous, 1–6 mm long. Secondary panicles similar to the primary one. Spikelets solitary, ellipsoid, 2.2–2.7 mm long, 0.8–0.9 mm wide, open at maturity, glabrous; lower glume lanceolate, 1.5–1.9 mm long, ⅔–¾ the length of the spikelet, acuminate, 1(–3)-nerved, a small stipe present between the lower and upper glume; upper glume and lower lemma subequal, 7–9-nerved, acute; lower palea lanceolate, 1.7–1.9 mm long, 0.4–0.7 mm wide, hyaline, glabrous; lower flower absent; upper anthecium long-ellipsoid, 2.1–2.3 mm long, 0.7–0.8 mm wide, papillose, with simple papillae evenly distributed, apiculate, the apex scabrous, otherwise glabrous; lodicules 2, cuneiform, truncate, ca. 0.2 mm long; stamens 3, the anthers 1.2 mm long; stigmas plumose, purplish. Caryopsis ellipsoid, brownish, 1.4 mm long, 0.7 mm wide; hilum oblong; embryo less than ½ the length of the caryopsis.

Paratypes. BRAZIL. RIO DE JANEIRO: Teresópolis, Serra dos Orgãos, Pedra do Sino, 2,100–2,170 m, Feb. 1953, *J. Vidal II-6467, II-6485* (R, SI).

Panicum cucaense is related to *P. petropolitanum* but is distinguished by its cespitose habit; erect, many-noded culms; strongly distichous leaf sheaths; stiff and folded leaf blades; and shortly exserted panicles.

Panicum petropolitanum differs from *P. cucaense* in its stoloniferous habit; culms geniculate, rooting and branching at the lower nodes, then becoming erect, few-noded; leaf blades linear-lanceolate, flat; and inflorescence with a peduncle to 16 cm long.

Panicum cucaense inhabits open and dry habitats in rocky, granitic soils of high-altitude campos of the mountains in eastern Brazil. Eiten (1978) indicated that these rocky areas over 2,000–2,500 m (planaltos), found on mountains such as Itatiaia or the Serra dos Orgãos and with frosts occurring at night in the cold season, should be distinguished from the campos rupestres, which occur from Bahia to the state of São Paulo at lower elevations.

Panicum petropolitanum Zuloaga & Morrone, sp. nov. TYPE: Brazil. Rio de Janeiro: Mun. Petrópolis, Araras, base da Pedra Maria Comprida, saxícola, heliófila, crescendo em beira de rio, 23 Mar. 1968, *D. Sucre & P. J. Braga 2553* (holotype, RB). Figure 6.

Panicum cucaense affine sed stoloniferum, vaginis non conspicue distichis, foliis planis et paniculis longe pedunculatis differt.

Plants perennial?, stoloniferous. Culms geniculate, rooting and branching at the lower nodes, then becoming erect, freely branching, 10–25 cm tall, few-noded; internodes 1–4 cm long, cylindric to compressed, hollow, glabrous; nodes compressed, brownish, covered with long hairs or glabrous. Sheaths striate, 1.5–5.5 cm long, longer than the internodes, one of the margins long-ciliate with whitish hairs, the other membranous or with long hairs near the ligule, glabrous on the rest of the surface; collar brownish, glabrous; ligules membranous-ciliate, ca. 0.2 mm long; blades linear-lanceolate, 2–7 cm long, 0.1–0.3 cm wide, flat, glabrous, the margins scaberulous, the apex attenuate. Panicles lax, diffuse, 2–6 cm long, 1–3.5 cm wide; peduncles to 16 cm long; rachis wavy, cylindric, glabrous, the branches alternate, divergent and distant, the axes of the branches glabrous; axils of the branches glabrous; pedicels triquetrous, scaberulous, 1–7 mm long. Spikelets solitary, long-ellipsoid, 2.4–2.6 mm long, 0.9 mm wide, glabrous, without a stipe; lower glume 1.8–2 mm long, ¾ the length of the spikelet, lanceolate, 1(–3)-nerved, the midnerve scabrous toward the apex; upper glume (7–)9-nerved, acute, embracing the lower lemma; upper glume and lower lemma subequal; lower lemma 9-nerved, embracing the upper anthecium; lower palea lanceolate, 1.5 mm long, 0.3–0.4 mm wide, hyaline, glabrous; lower flower absent; upper anthecium long-ellipsoid, 2.3 mm long, 0.7 mm wide, glabrous, shiny, with simple papillae evenly distributed all over its surface; upper lemma apiculate, the apicule ca. 0.2 mm long, pilose; lodicules 2, truncate, ca. 0.3 mm long, embracing the lower margins of the palea; stamens 3, the anthers 1 mm long; stigmas plumose. Caryopsis ellipsoid, 1.2 mm long, 0.6 mm wide; hilum punc-

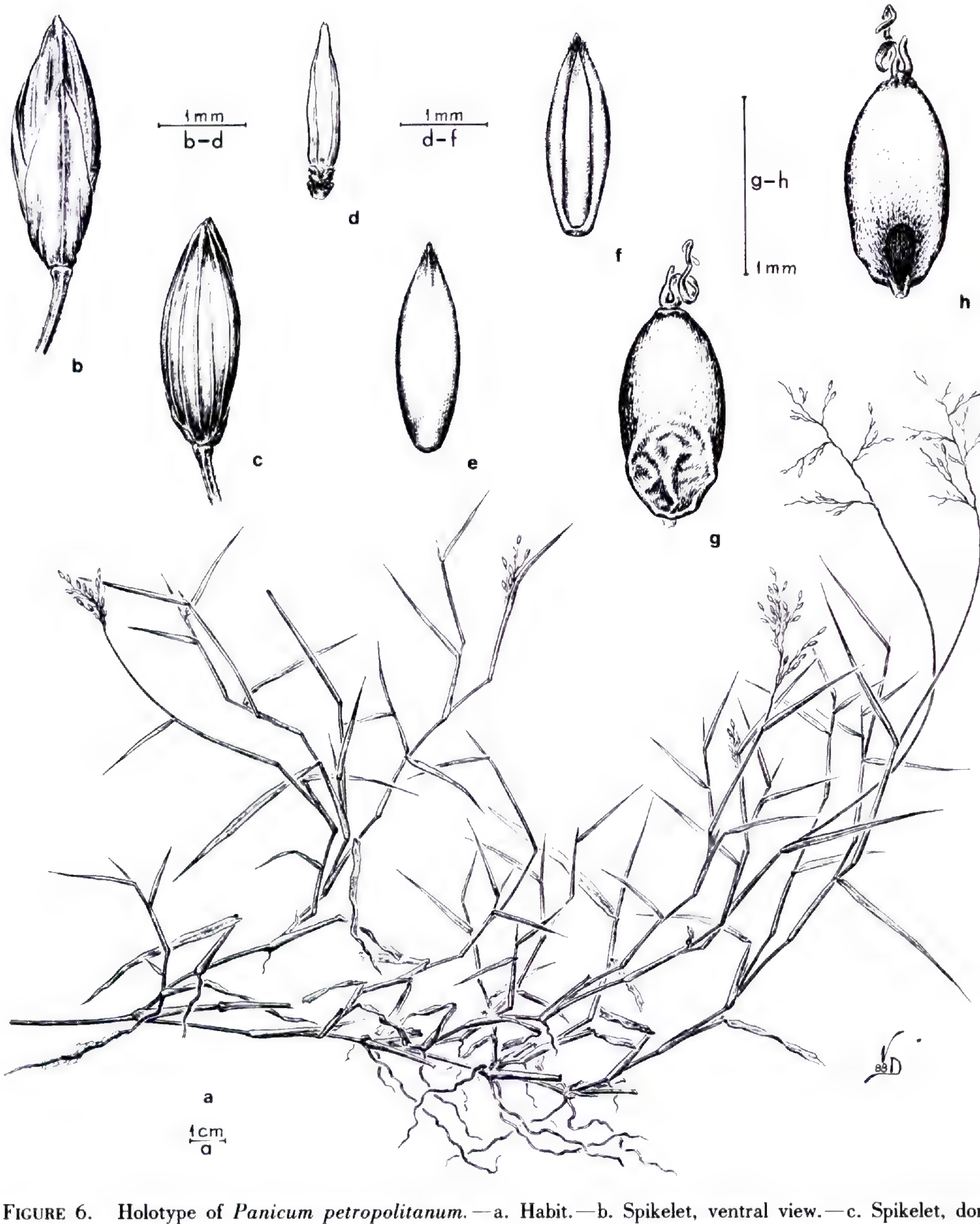

FIGURE 6. Holotype of *Panicum petropolitanum*.—a. Habit.—b. Spikelet, ventral view.—c. Spikelet, dorsal view.—d. Lower palea.—e. Upper anthecium, dorsal view.—f. Upper anthecium, ventral view.—g. Caryopsis, embryo side.—h. Caryopsis, hilum side.

tiform; embryo less than ⅓ the length of the caryopsis.

Panicum petropolitanum is a delicate plant that grows on rocky soils in open and humid places in borders of streams. See the discussion under *P. cucaense*.

Distinctions among the new species and related ones are summarized in the following key:

A. Upper glume and lower lemma 11–14-nerved; panicles 12–20 cm long.
  B. Spikelets 4.6–4.9 mm long, 1.6–1.7 mm wide; lower glume 5-nerved ..... *P. itatiaiae*
  BB. Spikelets 3–3.3 mm long, 1 mm wide; lower glume 3-nerved ..... *P. davidsei*

AA. Upper glume and lower lemma 7–9-nerved; panicles 1–16 cm long.
C. Leaf blades ovate-lanceolate to lanceolate, cordate, amplexicaulous, length : width ratio 3–5 : 1.
D. Panicles few-flowered, 1–2.5 cm long; leaf blades 1–2 cm long, 0.3–0.6 cm wide ... *P. cumbucana*
DD. Panicles multiflowered, 3–10 cm long; leaf blades 2–12 cm long, 0.5–1.8 cm wide.
E. Leaf blades with the margins long-ciliate, cartilaginous; lower glume to ½ (occasionally ⅔) the length of the spikelet ... *P. stipiflorum*
EE. Leaf blades with the margins ciliate only at the base, otherwise scabrous, not cartilaginous; lower glume ½ to ¾ the length of the spikelet ... *P. pycnoclados*
CC. Leaf blades linear to linear-lanceolate (lanceolate in *P. assurgens*), narrowed to subcordate, not amplexicaulous, length : width ratio 12–20 : 1.
F. Plants with conspicuous glands on the sheaths, blades and axes of the inflorescences; lower glume less than ⅓ the length of the spikelet ... *P. adenorhachis*
FF. Plants without glands (occasionally with a few glands on the axes of the inflorescences of *P. cucaense*), lower glume ½–⅘ the length of the spikelet.
G. Spikelets 2–2.3 mm long; lower glume to ½ the length of the spikelet ... *P. cabrerae*
GG. Spikelets 2.4–3.3 mm long; lower glume ⅔–⅘ the length of the spikelet.
H. Spikelets with a conspicuous stipe between the lower and upper glume.
I. Spikelets glabrous, 2.2–2.7 mm long; lower glume 1(–3)-nerved; leaf blades evenly distributed along the culms ... *P. cucaense*
II. Spikelets hirsute, 2.8–3.2 mm long; lower glume 5–7-nerved; leaf blades in fascicles at the top of the culms, these repeatedly branched ... *P. congestum*
HH. Spikelets without a stipe between the lower and upper glume.
J. Plants with culms 10–25 cm tall; blades 2–7 cm long, 0.1–0.3 cm wide; panicles 2–6 cm long; spikelets glabrous, 2.4–2.6 mm long ... *P. petropolitanum*
JJ. Plants with culms 50–200 cm tall; blades 4–12 cm long, 0.3–1 cm wide; panicles 4–16 cm long; spikelets pilose to glabrous, 2.6–3.3 mm long.
K. Spikelets hirsute, 2.6–3.1 mm long; leaf blades linear-lanceolate, rigid, 4–5(–12) cm long, 0.3(–1) cm wide ... *P. heliophilum*
KK. Spikelets glabrous to puberulous between the nerves, 3.3 mm long; leaf blades lanceolate, herbaceous, 8–12 cm long, 0.7–1 cm wide ... *P. assurgens*

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NEW SPECIES OF *CHUSQUEA* (POACEAE: BAMBUSOIDEAE) FROM COSTA RICA[1]

Yvonne Widmer[2] *and Lynn G. Clark*[3]

Abstract

Three new species of *Chusquea* from the upper montane forests of the Cordillera de Talamanca in Costa Rica are described and illustrated. *Chusquea tomentosa* and *C. subtilis* belong to *Chusquea* sect. *Longifoliae* L. G. Clark and are closely related to *C. foliosa* L. G. Clark. The third species, *C. talamancensis*, is a member of *Chusquea* sect. *Swallenochloa* (McClure) L. G. Clark and shows similarities to both *C. tonduzii* Hackel and *C. vulcanalis* (Soderstrom & C. Calderón) L. G. Clark. Revised keys to the species of sect. *Longifoliae* and sect. *Swallenochloa* in Costa Rica are provided.

Species of the woody bamboo genus *Chusquea* Kunth are often important components of montane forests in the New World (Veblen et al., 1977; Clark, 1989), but little ecological data relating to *Chusquea* is available. In Costa Rica, the upper montane forests along the Cordillera de Talamanca and volcanoes of the Cordillera Volcánica Central (northern slopes) are dominated by species of *Quercus* L., with a number of species of *Chusquea* found as elements in the understory or along the forest margins.

A Swiss Forestry Project, in association with the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) in Turrialba, Costa Rica, is developing a management plan for these forests. As part of this project, the ecology of two species of *Chusquea* in these forests was studied (Widmer, in prep.). When the two species began to flower in 1987–1989, we were able to confirm that they were both undescribed. Material of a third undescribed species in flower was also collected during the ecological study.

In this paper, we describe and illustrate the three new species, *C. tomentosa*, *C. subtilis*, and *C. talamancensis*. The first two species are members of *Chusquea* sect. *Longifoliae*, and the third belongs to *Chusquea* sect. *Swallenochloa*. Revised keys to the species of these two sections in Costa Rica are included.

Key to the Species of *Chusquea* sect. *Longifoliae* in Costa Rica
(based on vegetative specimens)

1a. Thin, curly leafless fibrillar branchlets interspersed with the normal, leafy subsidiary branches; internodes scabrous; foliage leaf blades with the base rounded to rounded-truncate ..... *C. scabra*

1b. Fibrillar branchlets absent; internodes usually smooth, rarely scabrous just below the nodes; foliage leaf blades with the base attenuate to rounded-attenuate.

2a. Foliage leaf blades 0.6–1.3 cm wide; subsidiary branches 18–30 per node; culm leaf sheaths 0.7–3 times as long as blades ..... *C. longifolia*

2b. Foliage leaf blades 0.3–0.9(–1.1) cm wide; subsidiary branches 24–80(–150) per node; culm leaf sheaths 1.5–10.5(–14) times as long as blades.

3a. Culm leaf sheaths abaxially scabrous to pilose, or sometimes glabrous; subsidiary branches 24–65 per node; inner ligules of foliage leaves 0.5–4 mm long; foliage leaf blades 0.4–0.9 cm wide ..... *C. patens*

3b. Culm leaf sheaths abaxially glabrous to pilose at the base; subsidiary branches 50–80(–150) per node; inner ligules of foliage leaves to 1.5 mm long; foliage leaf blades 0.3–0.7(–1.1) cm wide.

4a. Foliage leaf blades abaxially tomentose; fimbriae at the apex of foliage leaf sheaths straight, few per tuft ..... *C. tomentosa*

4b. Foliage leaf blades abaxially glabrous to sparsely pilose with scattered hairs; fimbriae at the

[1] Fieldwork was supported by the Swiss Directorate for Development Cooperation and Humanitarian Aid (Widmer) and the National Geographic Society (Clark).

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apex of foliage leaf sheaths often curly, several to many per tuft.
5a. Foliage leaf blades with the base attenuate, L : W = (26–)30–48(–54); culm leaf sheaths 4.4–6.6 times as long as the blades ..... *C. subtilis*
5b. Foliage leaf blades with the base rounded-attenuate, L : W = 20–40(–45); culm leaf sheaths 1.5–5.4 times as long as the blades ..... *C. foliosa*

KEY TO THE SPECIES OF *CHUSQUEA* SECT. *LONGIFOLIAE* IN COSTA RICA
(based on flowering specimens)

1a. Primary branches of panicle strongly spreading ..... *C. patens*
1b. Primary branches of panicles appressed or ascending.
2a. Sterile lemma II ¾–⅞ the spikelet length; thin, curly, leafless fibrillar branchlets interspersed with the normal, leafy subsidiary branches; internodes scabrous ..... *C. scabra*
2b. Sterile lemma II equalling or nearly equalling the spikelet length; fibrillar branchlets absent; internodes usually smooth, rarely scabrous just below the nodes.
3a. Spikelets 10.4–20.6 mm long; foliage leaf blades 0.6–1.3 cm wide; subsidiary branches 18–30 per node; culm leaf sheaths 0.7–3 times as long as the blades ..... *C. longifolia*
3b. Spikelets 8.4–15 mm long; foliage leaf blades 0.3–0.7(–1.1) cm wide; subsidiary branches 50–80(–150) per node; culm leaf sheaths 1.5–10.5(–14) times as long as the blades.
4a. Spikelets 11.5–15 mm long; sterile lemma I ⅝–⅔ the spikelet length; foliage leaf blades abaxially tomentose ..... *C. tomentosa*
4b. Spikelets 8.4–11.8 mm long; sterile lemma I ⅔–¾ the spikelet length; foliage leaf blades abaxially glabrous to sparsely pilose with scattered hairs.
5a. Spikelets 8.4–11.2 mm long; fertile lemma subulate; foliage leaf blades with the base rounded-attenuate, L : W = 20–40(–45) ..... *C. foliosa*
5b. Spikelets 9.8–11.8 mm long; fertile lemma aristate; foliage leaf blades with the base attenuate; L : W = (26–)30–48(–54) ..... *C. subtilis*

Chusquea tomentosa Widmer & L. G. Clark, sp. nov. TYPE: Costa Rica. Cartago: Villa Mills, road to Piedra Alta, 2,880 m, 30 May 1989 (fl), *Clark, Widmer & Stein 500* (holotype, CR; isotypes, ISC, MO, NY, US). Figure 1A–E.

Culmi 1.3–4 cm diam., 6–9 m alti. Folia culmorum 20.8–29 cm longa; vaginae 11.8–25.4 cm longae, 4–10.5(–14) plo longior quam laminae, abaxiales glabrae; laminae 1.4–5.4 cm longae, erectae, adaxiales pubescentes, abaxiales glabrae. Ramificatio infravaginalis. Vaginae foliorum fimbriatae, fimbriae paucae, 1–2 mm longae, rectae; laminae foliorum 15–27 cm longae, 0.3–0.7(–1.1) cm latae, L : W = 25–40, abaxiales tomentosae, non tessellatae. Paniculae 8–16 cm longae, angustae; rami laxe adpressi. Spiculae 11.5–15 mm longae, scaberulae. Glumae 2, squamiformes. Lemmata sterilia 2, subulata; lemma sterile I 7.2–9.7 mm longum; lemma sterile II 11.7–14 mm longum. Lemma fertile 11.5–13.5 mm longum, subulatum. Palea 9.5–12.1 mm longa, sulcata.

Culms 1.3–4 cm basal diam., 6–9 m tall, erect at the base, arching above and scandent. *Internodes* (11–14–)18–38(–51) cm long, more or less terete, shallowly sulcate above the central bud, usually smooth to scabrid below the node. *Culm leaves* 20.8–29 cm long, the juncture of the sheath and blade abaxially a ± horizontal and distinct line; sheaths 11.8–25.4 cm long, 4–10.5(–14) times as long as the blades, abaxially glabrous, the margins glabrous, one side occasionally minutely ciliate toward the apex; blades 1.4–5.4 cm long, triangular, erect, usually persistent, adaxially pubescent, abaxially glabrous, the apex subulate, the base narrower than the apex of the sheath; girdle 3–5 mm wide, densely pubescent; inner ligule 1–4 mm long, apically ciliolate. *Nodes* with one triangular central bud subtended by 50–60 subsidiary buds; sheath scar dipping away markedly below the bud/branch complement. *Branching* infravaginal; central bud developing tardily at the middle and upper nodes; leafy subsidiary branches 18–32 cm long, frequently rebranching basally, 60–80(–150) in the mature complement. *Foliage leaves* 4–9 per complement; sheaths glabrous, the overlapping margin ciliate, the apex with a tuft of fimbriae on either side of the summit, the fimbriae few per tuft, 1–2 mm long, straight, eventually deciduous; blades 15–27 cm long, 0.3–0.7(–1.1) cm wide, L : W = 25–40, adaxially glabrous, sometimes with some scattered hairs, abaxially tomentose and often glaucous, not tessellate, the apex short-setose, the base attenuate to rounded-attenuate; pseudopetiole 1–1.5 mm long; outer ligule an irregular, glabrous rim to 0.5 mm long; inner ligule to 1 mm long, truncate to rounded, pubescent. *Panicles* 8–16 cm long, narrow, the base often retained within the subtending sheath; rachis triquetrous, glabrous, the edges scabrid; branches loosely appressed, angular, scabrid, the lower ones 3–4 cm long; pedicels 2–6 mm long, angular, scabrid. *Spikelets* 11.5–15 mm long, scabrid. *Glumes* 2, scalelike, usually acute, nerves lacking

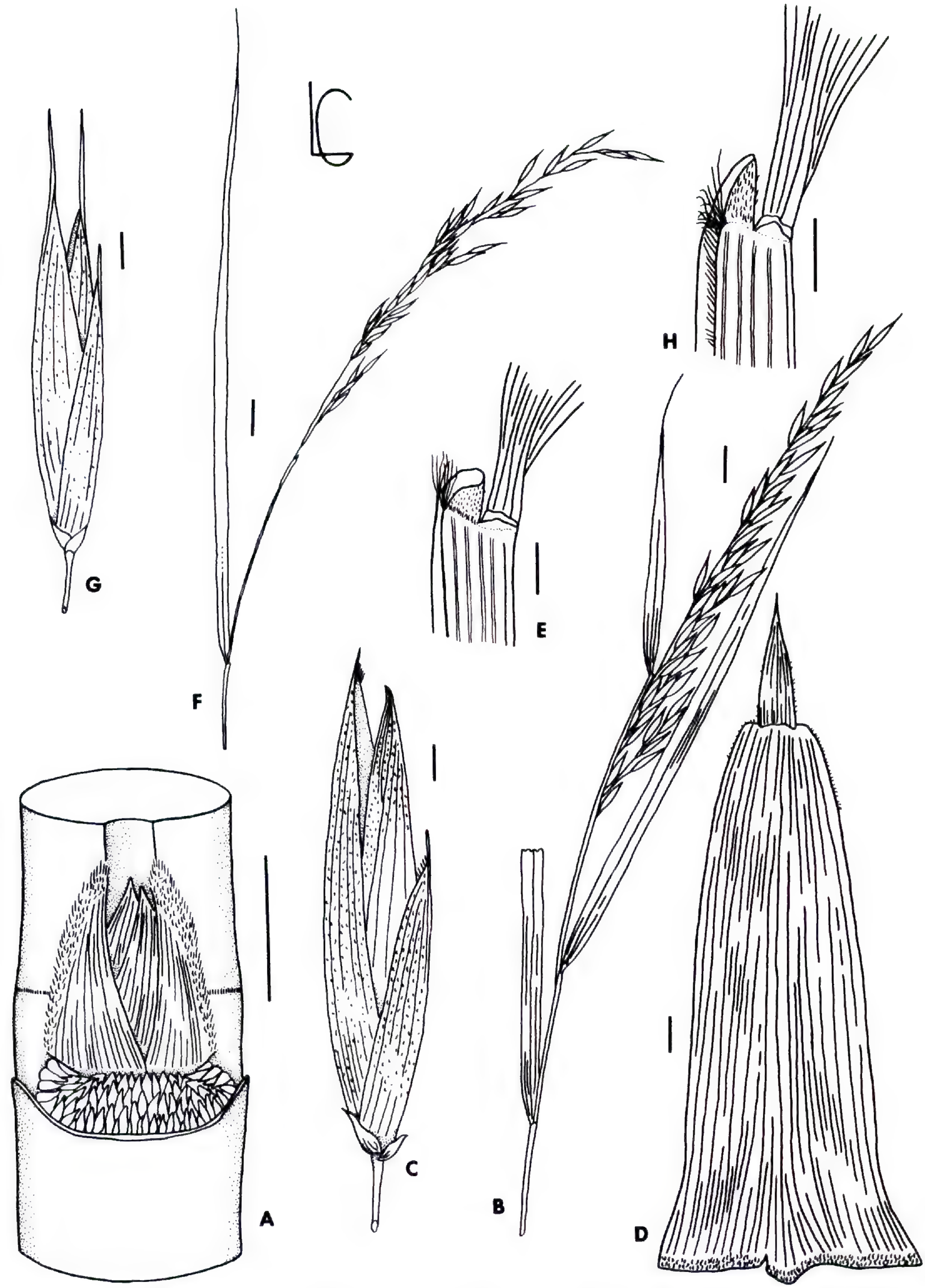

FIGURE 1. *Chusquea tomentosa* and *C. subtilis*. A–E. *C. tomentosa*.—A. Bud complement.—B. Panicle with subtending foliage leaves.—C. Spikelet.—D. Culm leaf, abaxial view.—E. Apex of foliage leaf sheath, showing inner and outer ligules, fimbriae, and pseudopetiole. (A, D based on *Clark & Clark 274*; B, E based on *Widmer 502*; C based on *Clark et al. 500*.) F–H. *C. subtilis*.—F. Panicle with subtending foliage leaf.—G. Spikelet.—H. Apex of foliage leaf sheath, showing inner and outer ligules, fimbriae, and pseudopetiole. (F–H based on *Widmer 508*.) A, B, D, F: bar equal to 1 cm; C, E, G, H: bar equal to 1 mm.

TABLE 1. A morphological comparison of *Chusquea foliosa*, *C. subtilis*, and *C. tomentosa*.

Character	*C. foliosa*	*C. subtilis*	*C. tomentosa*
Culm leaf sheath : blade	1.5–5.4	4.4–6.6	4–10.5(–14)
Foliage leaf sheath apex	fimbriae often curly, 1–2 mm long, many/tuft	fimbriae often curly, 1–1.5 mm long, many/tuft	fimbriae straight, 1–2 mm long, few/tuft
Foliage leaf length : width	20–40(–45)	(26–)30–48(–54)	25–40
Foliage leaf base	rounded-attenuate	attenuate	attenuate to rounded-attenuate
Foliage leaf abaxial pubescence	glabrous to sparsely pilose	glabrous to sparsely pilose	tomentose
Spikelet length	8.4–11.2 mm	9.8–11.8 mm	11.5–15 mm
Sterile lemma I/spikelet	2/3(–3/4)	2/3–3/4	5/8–2/3
Fertile lemma apex	subulate	aristate	subulate

or 1-nerved; glume I ca. 1/15 the spikelet length, 0.5–1.3 mm long; glume II ca. 1/10 the spikelet length, 0.7–1.5 mm long. *Sterile lemmas* 2, subulate, abaxially scabrid; sterile lemma I 5/8–2/3 the spikelet length, 7.2–9.7 mm long, 5- or 7-nerved; sterile lemma II extending the full spikelet length, 11.7–14 mm long, 5-, 7-, or 9-nerved. *Fertile lemma* 11.5–13.5 mm long, subulate, abaxially scabrid, 7–9-nerved. *Palea* 9.5–12.1 mm long, sulcate for most of the length, apiculate, scabrid, 6–8-nerved. *Stamens* 3; anthers 6–8 mm long. *Fruit* unknown.

Additional specimens examined. COSTA RICA. CARTAGO: S slope of Volcán Turrialba, 1–2 km E of Hacienda Central, *Pohl & Davidse 10867B* (ISC); Villa Mills, at Quebrada Voltea, *Widmer 500* (CR, ISC), *501* (CR, ISC); on the path to Cerros Cuericí, *Widmer 502, 503, 504, 506 & s.n.* (CR, ISC); La Esperanza del Guarco, Km 61.8 on the Carretera Interamericana, 4 km NE, 19 Jan. 1990 (fl), *Widmer 505* (CR, ISC). SAN JOSÉ: along the Carretera Interamericana between Km 77 & 78, *Clark & Clark 274* (ISC, MO, US); Cordillera de Talamanca, Km post 107, ca. 20 km N of San Isidro del General along the Carretera Interamericana, *Davidse 761* (ISC); Trinidad de Dota, Km 62.5 along the Carretera Interamericana, 6 Feb. 1990 (fl), *Widmer 507* (CR, ISC).

Chusquea tomentosa is characterized by the abaxially tomentose foliage leaf blades and the scabrid spikelets 11.5–15 mm long. This species occurs in the Cordillera de Talamanca in montane forests at elevations of 2,500 to 3,000 m. It grows on slightly drier sites with southern to southeastern exposures.

Vegetative specimens of *C. tomentosa* were previously assigned to *C. foliosa* L. G. Clark (Clark, 1989). With the advent of flowering in 1989, *C. tomentosa* could be clearly distinguished from *C. foliosa* based on the large spikelets. Vegetatively, the two species are very similar in overall aspect, but may be differentiated by the abaxially tomentose foliage leaf blades and the few, straight fimbriae at the apex of the foliage leaf sheaths of *C. tomentosa*. In *C. foliosa*, the foliage leaf blades are abaxially glabrous to sparsely pilose with scattered hairs, and the fimbriae are more numerous and usually curly. *Chusquea foliosa*, *C. tomentosa*, and *C. subtilis* form a complex of closely related species within sect. *Longifoliae*; a comparison of the three species is presented in Table 1.

Chusquea subtilis Widmer & L. G. Clark, sp. nov. TYPE: Costa Rica. Cartago: Villa Mills, El Sitio, confluence of Quebradas Siberia and Voltea, 2,550 m, 9 Dec. 1988 (fl), *Widmer 508* (holotype, CR; isotypes, CATIE/SBN, ISC, ZT). Figure 1F–H.

Culmi 1.5–3 cm diam., 2–6 m alti. Folia culmorum 19.7–24.3 cm longa; vaginae 17–20 cm longae, 4.4–6.6 plo longior quam laminae, abaxiales pilosae ad basim, glabrae ad apicem; laminae 2.6–4.5 cm longae, erectae, abaxiales sparsim pilosae. Ramificatio infravaginalis. Laminae foliorum (9–)12–21.6 mm longae, 0.3–0.6 cm latae, L : W = (26–)30–48(–54), abaxiales glabrae, non tessellatae. Paniculae (7–)11–18 cm longae, angustae; rami laxe adpressi. Spiculae 9.8–11.8 mm longae, scaberulae. Glumae 2, squamiformes. Lemmata sterilia 2; lemma sterile I 7.5–9.2 mm longum, subulatum; lemma sterile II 9.3–11.8 mm longum, subulatum-aristatum. Lemma fertile 10–11.7 mm longum, aristatum. Palea 7.4–9 mm longa, sulcata tantum ad apicem.

Culms to 1.5–3 cm diam., 2–6 m tall, erect at the base, arching above. *Internodes* to 35 cm long, terete, shallowly sulcate above the central bud, usually scabrid to smooth. *Culm leaves* 19.7–24.3 cm long, the juncture of the sheath and blade abaxially a ± horizontal and distinct line; sheaths 17–20 cm long, 4.4–6.6 times as long as the blades, abaxially pilose toward the base, glabrous toward the apex; blades 2.6–4.5 cm long, triangular, erect, persistent, adaxially antrorsely pu-

bescent between the nerves, abaxially sparsely pilose, the apex subulate, the base narrower than the apex of the sheath; girdle 0.5–1 cm wide, densely pilose; inner ligule 1–2 mm long, ciliolate. *Nodes* with one triangular central bud; sheath scar dipping away markedly below the bud/branch complement. *Branching* infravaginal; central bud developing tardily at the middle and upper nodes; leafy subsidiary branches to 34 cm long, occasionally rebranching basally, 70–80(–100) branches in the mature complement. *Foliage leaves* 3–5 per complement; sheaths glabrous, the overlapping margin ciliate, the apex with a tuft of fimbriae on either side of the summit, the fimbriae numerous per tuft, 1–1.5 mm long, usually curly; blades (9–)12–21.6 cm long, 0.3–0.6 cm wide, L : W = (26–)30–48(–54), adaxially usually glabrous, sometimes with scattered hairs near the midrib, abaxially glabrous, sometimes with scattered hairs, not tessellate, the apex short setose, the base attenuate; pseudopetiole 1–2 mm long, not distinct; outer ligule a minute, glabrous rim 0.1–0.3 mm long; inner ligule to 1 mm long, rounded to irregular, abaxially basally pubescent. *Panicles* (7–)11–18 cm long, narrow, fully exserted from the subtending sheath; rachis triquetrous, glabrous, the edges glabrous to scabrid; branches loosely appressed, angular, glabrous, the lower ones 2–4.5 cm long; pedicels 1–7 mm long, angular, glabrous. *Spikelets* 9.8–11.8 mm long, scabrid. *Glumes* 2, scalelike, nerves lacking; glume I ca. 1/20 the spikelet length, 0.5–0.8 mm long; glume II ca. 1/15 the spikelet length, 0.6–1 mm long. *Sterile lemmas* 2, abaxially scabrid-pubescent, (5–)7-nerved; sterile lemma I 2/3–3/4 the spikelet length, 7.5–9.2 mm long, subulate; sterile lemma II equalling or nearly equalling the spikelet length, 9.3–11.8 mm long, subulate-aristate. *Fertile lemma* 10–11.7 mm long, aristate, abaxially scabrid-pubescent, 7-nerved. *Palea* 7.4–9 mm long, sulcate only toward the apex, apiculate, scabrid, 4- or 6-nerved. *Stamens* 3; anthers 4.2–5.2 mm long. *Fruit* a caryopsis, 4.7–6 mm long, flattened, grooved along the hilum, the hilum dark reddish brown, the style base persistent.

Additional specimens examined. COSTA RICA. CARTAGO: Cordillera de Talamanca, on the path to Cerros Cuericí, *Clark, Widmer & Stein 503* (CR, ISC, MO, NY, US); Villa Mills, Quebrada Voltea, 9 Dec. 1988 (fl), *Widmer 509* (CR, ISC); 19 Aug. 1989 (fl), *Widmer 511* (CR, ISC); 15 Nov. 1989 (fl), *Widmer 513* (CR, ISC); Cerro Abarca, near Río Angeles, 18 Jan. 1989 (fl), *Widmer 510* (CR, ISC); Cuericí, 9 Nov. 1989 (fl), *Widmer 512* (CR, ISC); Villa Mills, El Sitio, confluence of the Quebradas Voltea and Siberia, 15 Nov. 1989 (fl), *Widmer 514* (CR, ISC). SAN JOSÉ: Villa Mills, S of La Georgina, 15 Dec. 1978 (fl), *Pohl & Gabel 13725* (ISC, MO).

The specific epithet of *C. subtilis* refers to the fine leaves and delicate aspect of the panicles. This species is characterized by the narrow foliage leaf blades and scabrid-pubescent spikelets 9.8–11.8 mm long with the fertile lemma aristate (Table 1). *Chusquea subtilis* occurs in the Cordillera de Talamanca in montane forests along streams or at humid sites at elevations of 2,550 to 3,000 m.

KEY TO THE SPECIES OF *CHUSQUEA* SECT. *SWALLENOCHLOA* IN COSTA RICA
(based on vegetative specimens)

1a. Foliage leaf blades 0.4–0.6 cm wide ..... *C. paludicola*
1b. Foliage leaf blades 0.7–2.4 cm wide.
  2a. Inner ligule of foliage leaves 1–7 cm long, tapering.
    3a. Culm leaf sheaths (1.5–)4.5–7 times as long as the blades, the blades adaxially glabrous; foliage leaf blades usually yellowish green ..... *C. amistadensis*
    3b. Culm leaf sheaths 5–13 times as long as the blades, the blades adaxially pubescent; foliage leaf blades green ..... *C. longiligulata*
  2b. Inner ligule of foliage leaves 0.5–4(–15) mm long, truncate to tapering.
    4a. Foliage leaf blades 3–14.5 cm long; culm leaf blades 0.35–1.5 cm long, the sheaths (7–)12–27 times as long as the blades ..... *C. subtessellata*
    4b. Foliage leaf blades (5.5–)10–29 cm long; culm leaf blades 1–6.5 cm long, the sheaths (1.5–)2–11 times as long as the blades.
      5a. Foliage leaf blades with L : W = 7–12(–17), the base rounded to rounded-truncate ..... *C. vulcanalis*
      5b. Foliage leaf blades with L : W = (7–)10–20(–24), the base rounded to attenuate.
        6a. Inner ligules of foliage leaves 1–2.5 mm long, truncate to rounded; foliage leaf sheaths often farinose, especially when young; culm leaf blades adaxially scabrid ..... *C. talamancensis*
        6b. Inner ligules of foliage leaves (2–)3–15 mm long, usually tapering; foliage leaf sheaths not farinose; culm leaf blades adaxially pubescent ..... *C. tonduzii*

KEY TO THE SPECIES OF *CHUSQUEA* SECT. *SWALLENOCHLOA* IN COSTA RICA
(based on vegetative and flowering specimens)

1a. Foliage leaf blades 0.4–0.6 cm wide ..... *C. paludicola*
1b. Foliage leaf blades 0.7–2.4 cm wide.

2a. Panicles open, pyramidal, with stiffly spreading branches ..... *C. tonduzii*
2b. Panicles ± congested, often spicate, narrow, with appressed or ascending branches.
3a. Spikelets glabrous, often slightly falcate; inner ligules of foliage leaves 1–7 cm long, tapering.
4a. Foliage leaf blades 14–33 cm long, 0.7–2.3 cm wide, L : W = 9–25, green; culm leaf sheaths 5–13 times as long as the blades, the blades adaxially pubescent ..... *C. longiligulata*
4b. Foliage leaf blades 6–20.5 cm long, 0.7–1.4(–1.8) cm wide, L : W = 7–14.5(–16), usually yellowish green; culm leaf sheaths (1.5–)4.5–7 times as long as the blades, the blades adaxially glabrous ..... *C. amistadensis*
3b. Spikelets with some degree of pubescence, linear; inner ligules of foliage leaves 0.5–4(–7.5) mm long, rounded to truncate.
5a. Panicles narrow, spicate, the branches appressed; foliage leaf blades 3–14.5 cm long, 0.7–1.3 cm wide; culm leaf blades 0.35–1.5 cm long, the sheaths (7–)12–27 times as long as the blades ..... *C. subtessellata*
5b. Panicles somewhat narrow but not spicate, the branches loose and ascending but not tightly appressed; foliage leaf blades (5.5–)10–29 cm long, 1–2.4 cm wide; culm leaf blades 1.5–6.5 cm long, the sheaths (1.5–)2–11 times as long as the blades.
6a. Foliage leaf blades with L : W = 7–12(–17), the base rounded to rounded-truncate, the sheaths not farinose; spikelets completely pubescent ..... *C. vulcanalis*
6b. Foliage leaf blades with L : W = (8–)10–20(–24), the base rounded to attenuate-rounded, the sheaths often farinose, especially when young; spikelets scabrid-pubescent except toward the bases of the bracts ..... *C. talamancensis*

Chusquea talamancensis Widmer & L. G. Clark, sp. nov. TYPE: Costa Rica. Cartago: Cordillera de Talamanca, on the path to Cerros Cuericí, 3,030 m, 30 May 1989 (fl), *Clark, Widmer & Stein 502* (holotype, CR; isotypes, ISC, MO, NY, US). Figure 2A–F.

Culmi 0.7–3.8 cm diam., 3–6(–9) m alti. Folia culmorum 15–24 cm longa, farinosae initio; vaginae 10.6–18 cm longae, (1.5–)2–11 plo longior quam laminae, abaxiales glabrae; laminae 1.5–6.5 cm longae, erectae, adaxiales scaberulae, abaxiales glabrae. Ramificatio intravaginalis. Vaginae foliorum plerumque farinosae initio; laminae foliorum 13–29 cm longae, 1–1.8 cm latae, L : W = (8–)10–20(–24), glabrae, abaxiales tessellatae. Paniculae 11–29 cm longae, angustae; rami laxe adpressi. Spiculae 5.6–7.5 mm longae, pubescentes. Glumae 2, squamiformes. Lemmata sterilia 2, subulata; lemma sterile I 4.2–5 mm longum; lemma sterile II 5.3–6.3 mm longum. Lemma fertile 6–7.1 mm longum, apiculatum. Palea 5.6–6.2 mm longa, sulcata ad apicem.

Culms 0.7–3.8 cm basal diam., 3–6(–9) m tall, erect at the base, arching above. *Internodes* (17–19)27–37(–43) cm long, ± terete, smooth, waxy to farinose. *Culm leaves* 15–24 cm long, the juncture of the sheath and blade an irregular, slightly sloping line, abaxially indistinct, farinose when young; sheaths 10.6–18 cm long, (1.5–)2–11 times as long as the blades, abaxially glabrous; blades 1.5–6.5 cm long, erect, persistent, apiculate, adaxially scabrid, abaxially glabrous; girdle 1–6 mm wide, glabrous; corky ridge present at the juncture of the sheath and girdle; inner ligule 1–2 mm long, stiff, glabrous, irregular. *Nodes* with one triangular central bud subtended by 5–11 subsidiary buds; sheath scar dipping slightly below the branch complement. *Branching* intravaginal; leafy subsidiary branches 35–69 cm long, frequently rebranching basally; 7–30 branches in the mature complement. *Foliage leaves* 6–11 per complement; sheaths glabrous, often farinose especially when young; blades 13–29 cm long, 1–1.8(–2.4) cm wide, L : W = (8–)10–20(–24), adaxially and abaxially glabrous, abaxially tessellate, the apex acuminate to short setose, the base rounded to attenuate-rounded; pseudopetiole 2–4 mm long; outer ligule a stiff, glabrous rim 0.3–1 mm long; inner ligule 1–2.5 mm long, truncate to rounded, glabrous, chartaceous. *Panicles* 11–29 cm long, narrow but not spicate, often the base not exserted from the subtending sheath; rachis somewhat complanate, glabrous to scabrid, the edges scabrid; branches loosely appressed, ascending, angular, scabrous, the lower ones 3–9 cm long; pedicels 1.5–4 mm long, angular, scabrid. *Spikelets* 5.6–7.5 mm long. *Glumes* 2, scalelike, abaxially scabrid to pubescent; glume I ca. 1/10 the spikelet length, 0.6–1 mm long, nerves absent or 1-nerved; glume II ca. 1/5 the spikelet length, 0.9–1.6 mm long, 1-nerved. *Sterile lemmas* 2, subulate, abaxially pubescent on the upper 1/2–2/3, otherwise glabrous; sterile lemma I ca. 2/3 the spikelet length, 4.2–5 mm long, 3- or 5-nerved; sterile lemma II ca. 9/10 the spikelet length, 5.3–6.3 mm long, 5-nerved. *Fertile lemma* 6–7.1 mm long, apiculate, abaxially pubescent on the upper 1/2–1/3, otherwise glabrous, 7- or 9-nerved. *Palea* 5.6–6.2 mm long, sulcate toward the apex, the sulcus pubescent, 4-nerved. *Stamens* not seen. *Fruit* a caryopsis.

Additional specimens examined. COSTA RICA. CARTAGO: along the Carretera Interamericana just below páramo, *Clark & Clark 273* (ISC, MO, US); Villa Mills, road to Piedra Alta, *Clark et al. 501* (CR, ISC, MO, NY, US); along Interamerican Highway near Cerro de la Muerte, *Fisher R354* (US). CARTAGO/SAN JOSÉ: Cerro Jaboncillo, along access road to transmission line tower on summit,

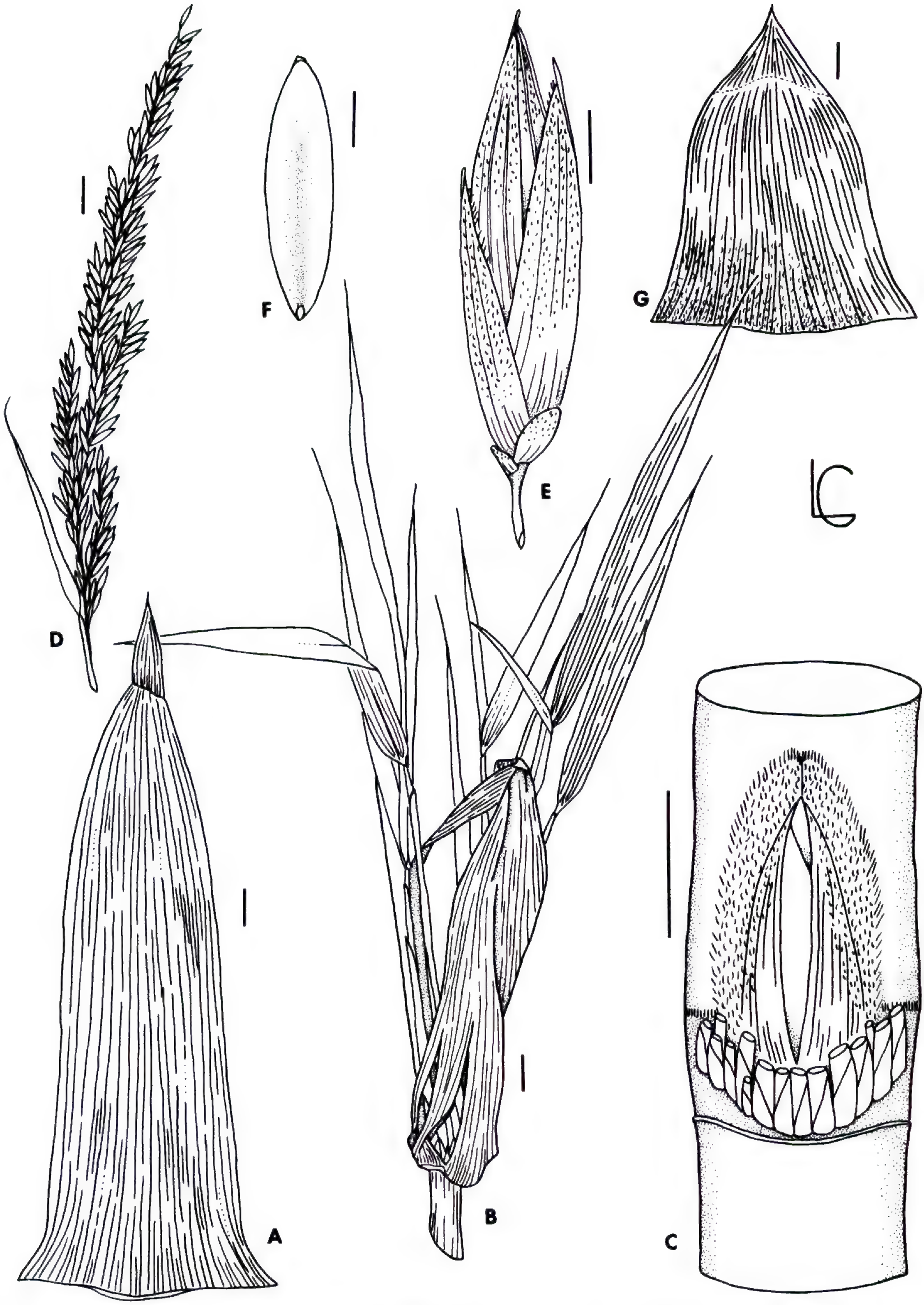

FIGURE 2. *Chusquea talamancensis* and *C. tonduzii*. A–F. *C. talamancensis*.—A. Culm leaf, abaxial view.—B. Branch complement and foliage leaves.—C. Bud/branch complement.—D. Panicle.—E. Spikelet.—F. Caryopsis. (A–C based on *Clark & Clark 273*; D based on *Pohl 15676*; E based on *Clark et al. 502*; F based on *Widmer s.n.*)—G. *C. tonduzii*, culm leaf, abaxial view (based on *Clark et al. 497*). A–D, G: bar equal to 1 cm; E–F; bar equal to 1 mm.

TABLE 2. A morphological comparison of *Chusquea vulcanalis*, *C. talamancensis*, and *C. tonduzii*.

Character	*C. vulcanalis*	*C. talamancensis*	*C. tonduzii*
Culm leaf sheath, abaxial	glabrous	glabrous	only basal ½ pubescent to completely glabrous
Culm leaf blade, adaxial	glabrous to scabrid	scabrid	densely pubescent
Foliage leaf blade color	yellowish green	green	green
Foliage leaf blade width	(0.7–)1.1–2.4 cm	1–1.8(–2.4) cm	(0.7–)1–1.5 cm
Foliage leaf length : width	7–12(–17)	(8–)10–20(–24)	(7–)10–19.5
Foliage leaf inner ligule length	1–4(–7.5) mm	1–2.5 mm	(2–)3–15 mm
Foliage leaf sheath	not farinose	often farinose when young	not farinose
Panicle shape	narrow	narrow	pyramidal
Spikelet length	5.7–8.5 mm	5.6–7.5 mm	(5.4–)6–7.6 mm
Spikelet pubescence	completely pubescent	scabrous/pubescent except glabrous toward bases of bracts	glabrous except bracts abaxially apically pubescent
Sterile lemma I/spikelet	¾–⅞	⅔	½
Sterile lemma II/spikelet	(⅘–)1	⅘	⅔

Cerro de la Muerte, *Horn 129, 130* (ISC); power lane 1 km W of Cerro Jaboncillo, Cerro de la Muerte, *Horn 242* (ISC). LIMÓN: on the path to Cerro Chirripó, 2 Apr. 1989 (fl), *Widmer 517* (ISC). PUNTARENAS: Cordillera de Talamanca, upper slopes of Cerro Echandi, *Davidse et al. 23885, 23961* (ISC, MO). SAN JOSÉ: La Georgina, roadside W of Carretera Interamericana, E of restaurant, forest margin, 28 Jan. 1989 (fl), *Pohl 15676* (ISC, MO); La Georgina, *Pohl & Clark 13924* (ISC, MO); La Georgina, opposite the restaurant, *Pohl & Clark 14627* (ISC).

Chusquea talamancensis is characterized by the often farinose foliage leaf sheaths, green foliage leaf blades with the inner ligules 1–2.5 mm long, and pubescent spikelets with sterile lemma II ⅔ the spikelet length. As indicated by the specific epithet, this species is found in the Cordillera de Talamanca, in upper montane forests at elevations of 2,600 to 3,200 m, usually on northern or northwestern exposures.

Vegetative specimens of *C. talamancensis* were previously assigned to *C. tonduzii* Hackel (Clark, 1989), even though the inner ligules were much shorter than is typical for *C. tonduzii*. The panicle and spikelets of *C. talamancensis* are very similar to those of *C. vulcanalis*, from which it is vegetatively distinct. The three species are compared in Table 2. The description of the culm leaves of *C. tonduzii* in Clark (1989) is based on specimens of *C. talamancensis*. A complete recent vegetative collection of *C. tonduzii* (*Clark et al. 497*) showed that its culm leaves are very similar to those of *C. paludicola* L. G. Clark (Fig. 2G), but the blades of *C. tonduzii* are adaxially pubescent as in *C. longiligulata* (Soderstrom & Calderón) L. G. Clark.

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PANAMANTHUS, A NEW MONOTYPIC GENUS OF NEOTROPICAL LORANTHACEAE[1]

Job Kuijt[2]

ABSTRACT

The monotypic genus *Panamanthus* Kuijt (*P. panamensis* (Rizz.) Kuijt) is proposed to accommodate the Panamanian mistletoe previously known as *Struthanthus panamensis* (Rizz.) Barlow & Wiens; an expanded description and illustrations are provided. It is suggested that *Panamanthus* is related to *Gaiadendron* G. Don, another monotypic genus found in approximately the same ecological zone.

The mistletoe species known presently as *Struthanthus panamensis* (Rizz.) Barlow & Wiens was originally described as a member of the genus *Phrygilanthus* (Rizzini, 1960). As made clear by Barlow & Wiens (1973), Eichler's genus *Phrygilanthus* cannot be maintained for systematic and nomenclatural reasons. The only species of *Phrygilanthus* that Rizzini mentioned as a possible relative to his new species has subsequently been removed to *Psittacanthus* (*Psittacanthus palmeri* (S. Watson) Barlow & Wiens; Barlow & Wiens, 1973). Rizzini's species was transferred to *Struthanthus* by Barlow & Wiens (1973), although these authors did recognize its unusual nature.

There are two major morphological features in which Rizzini's species differs from all other known species of *Struthanthus*. First, it has bisexual flowers, whereas the other species are strictly dioecious. Second, the inflorescence is consistently monadic, while that of the other species is basically or entirely triadic. Also, the prophyllar bracteoles associated with each flower are fused above the flower so as to hide the entire ovary, a feature not known in any other neotropical continental Loranthaceae. The first two features are elsewhere in the New World known only in *Oryctanthus* Eichl., *Oryctina* Van Tiegh., *Maracanthus* Kuijt, and the Caribbean *Dendropemon* Blume, and strict logic would necessitate placement of Rizzini's species in one of those genera. Of these, only the last genus needs to be considered, as various other structural characters prohibit placement in any of the first three. *Dendropemon* often has pedunculate monads, and the bracteoles are sometimes fused in a cupulate fashion. The anthers of Rizzini's species are nearly dorsifixed, but *Dendropemon* has unequivocally basifixed anthers. Also, the filaments of *Dendropemon* are laterally excavated, a feature shared with the continental *Phthirusa* but not with other genera. The stem roots of Rizzini's species have no equivalent in *Dendropemon*, and it would be extraordinary to have a low-elevation, strictly Caribbean genus represented by a single species at high elevations in Chiriquí. No one has suggested affinities to *Dendropemon*, however, which is clearly very closely related to *Phthirusa* and probably to *Oryctanthus* as well; the species would clearly be out of place there at least as much as it has been in *Struthanthus*. The disposition of *S. panamensis* has been a continual problem since its description, and I here propose that the species be treated as a monotypic genus with possible, but rather distant affinities to another monotypic genus found in the same ecological zone, i.e., *Gaiadendron*.

Panamanthus Kuijt, gen. nov. TYPE: *Panamanthus panamensis* (Rizz.) Kuijt, comb. nov.

Phrygilanthus panamensis Rizz., Ann. Missouri Bot. Gard. 47: 270–272. 1960.

Struthanthus panamensis (Rizz.) Barlow & Wiens, Brittonia 25: 39. 1973.

[1] I acknowledge continuing financial support from the Natural Sciences and Engineering Research Council of Canada. Karel U. Kramer of Zürich kindly provided the Latin diagnosis. Several collectors have made special efforts in Chiriquí to collect this elusive species, and several curators have extended special courtesies; these efforts have added significant substance to this presentation.

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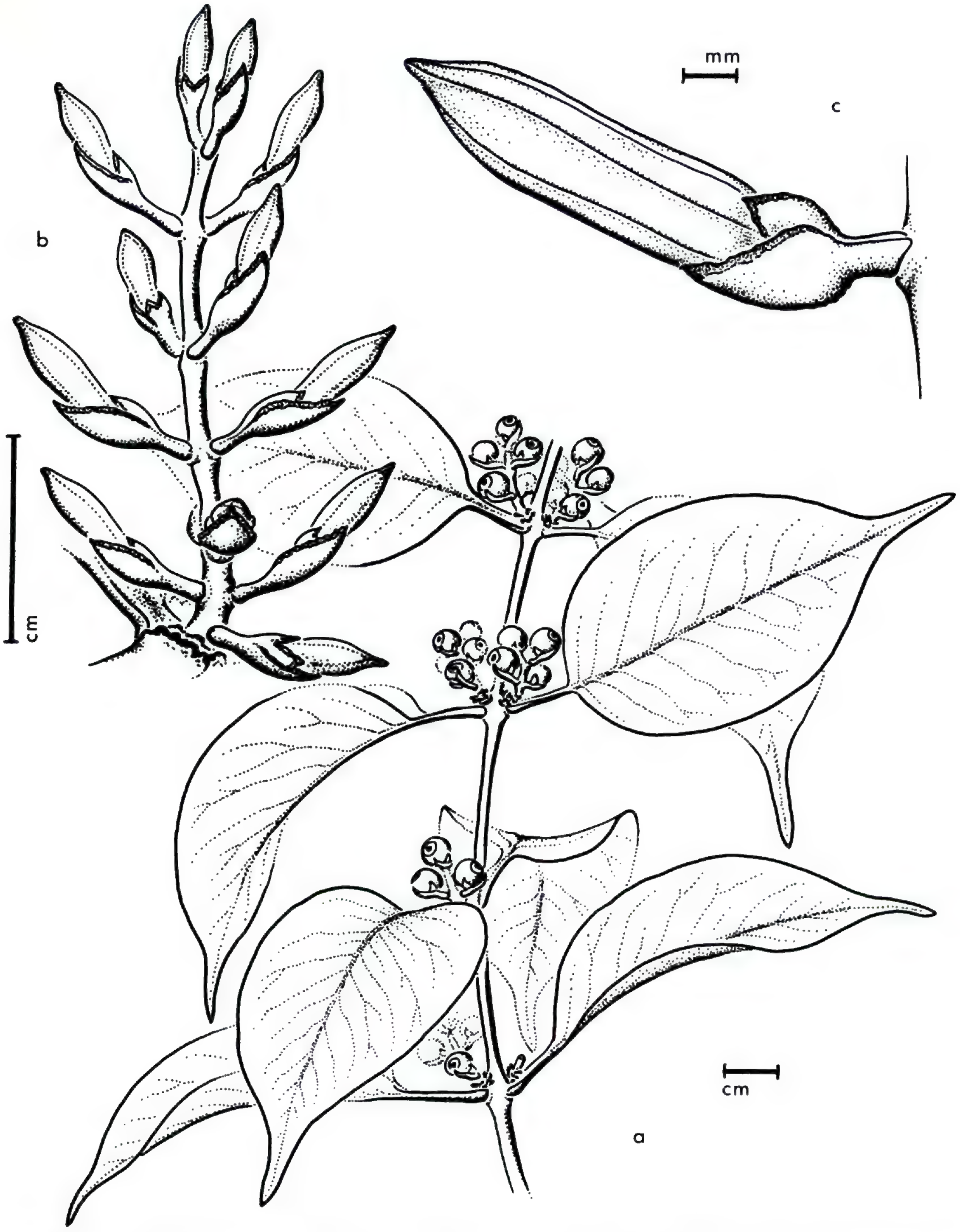

FIGURE 1. *Panamanthus panamensis.*—a. Habit of plant in fruit.—b. Inflorescence in bud.—c. Monad in bud (a, *van der Werff & Herrera 6330*, LEA; b, c, *McPherson 9380*, LEA).

Inflorescentia indeterminata, monadica, bracteis numerosis caducis suffulta; flores hermaphroditi, bracteolae coalitae, cupulam formantes et ovarium occultantes.

Scandent plants to 3 m diam., with rather straight, pendant branches 1 m or more in length, with occasional epicortical roots formed from branches; internodes to 6 cm long, somewhat quadrangular when young, soon becoming terete. Leaves to 14 × 7 cm, decussate; petiole 1.5 cm long, blade thin, with evident pinnate venation, base

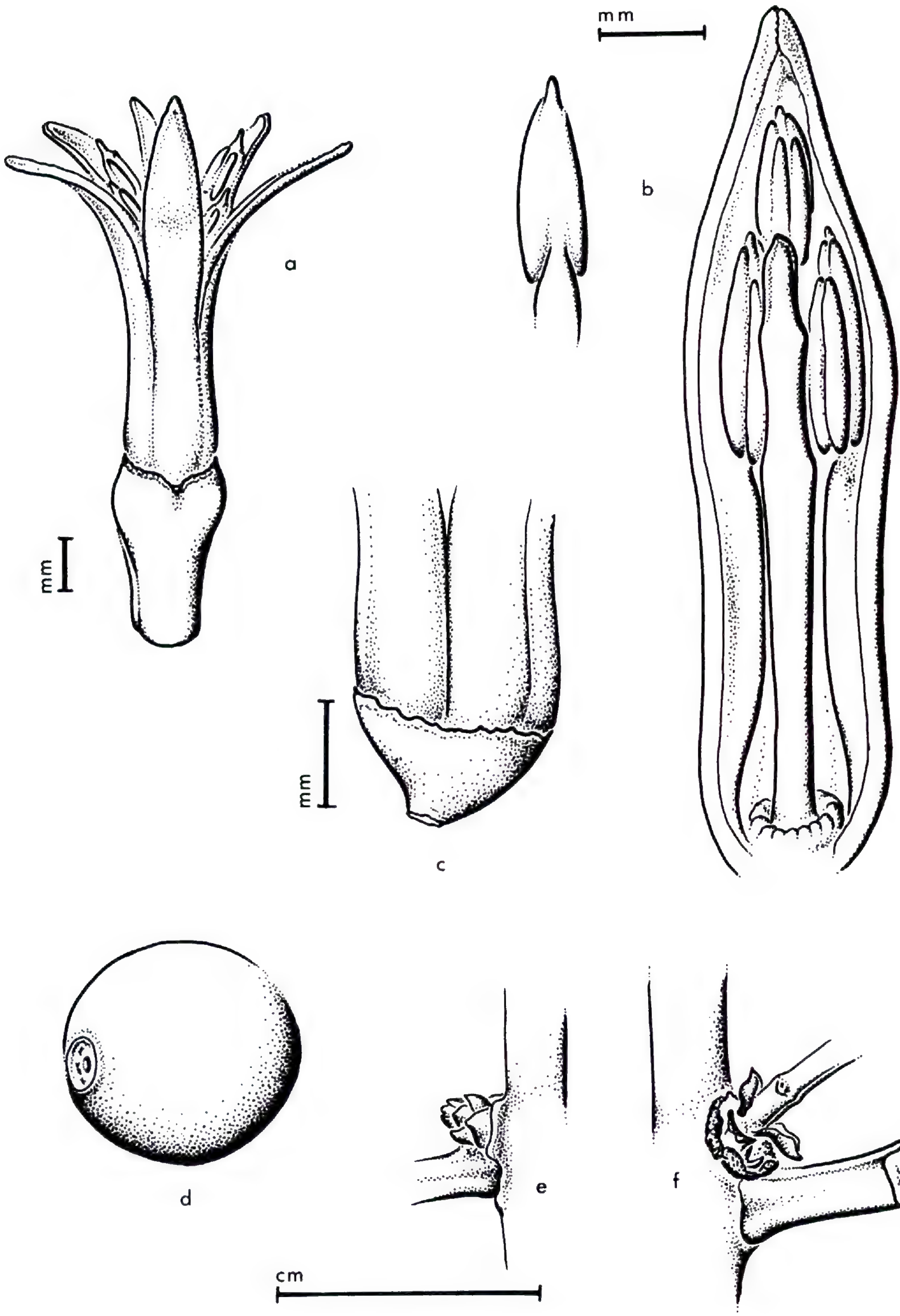

FIGURE 2. *Panamanthus panamensis*.—a. Open flower, the two fused bracteoles visible below.—b. Longitudinal section of mature bud, with stamen shown separately, dorsal view.—c. Base of flower.—d. Mature fruit.—e. Young inflorescence bud still covered by scale leaves.—f. Base of infructescence with old persistent scale leaves (a–c, *McPherson 9380*, LEA; d, *Wilbur & Teeri 13109*, DUKE; e, f, *Luteyn 3786*, DUKE).

truncate or very obtuse, apex contracted into conspicuous, slender tail to 1.5 cm long. Inflorescences 2–4 cm at anthesis, somewhat quadrangular, racemose, indeterminate, in small axillary clusters, individually subtended by several pairs of caducous scale leaves and set in a craterlike corky rim, inflorescence peduncle very short (2–3 mm), followed by 6–8 pairs of monads; monad peduncle 2–2.5 mm long, fused along its length with a bract extending 4 mm beyond and sharply acute; bracteoles ca. 2 mm long, fused along the lower ⅔ of their length where investing the nearly hidden ovary, the free, acute tips 1 mm long; both bracteoles and bracts with conspicuous whitish margins when dry; infrutescence elongating to 6–9 cm at maturity. Flowers hexamerous, pale yellow, with pleasant odor, the petals very slightly dimorphic; mature bud 8–9 mm long, thickest (2 mm) just above the middle, with prominently acute tip; ovary very short (1 mm), calyculus inconspicuous, with slightly undulating rim; anthers dimorphic, basifixed or nearly so, lower ones reaching to top of stigma, upper ones almost entirely beyond; pollen sacs four, long and slender, connective extending beyond as a small spur; filament extremely short (0.5 mm), continuing downward as a long buttress on petal. Pollen isopolar, diplosyndemicolpate, glabrate. Style straight, ca. 5 mm long, terete below but compressed by the anthers above; stigma undifferentiated, sometimes slightly oblique. Nectary prominent, with somewhat undulating surface. Fruit baccate, nearly 1 cm diam., spherical, yellowish orange, its calyculus inconspicuous, viscin tissue insignificant. Embryo small (2 mm long), slender, lacking a swollen radicular apex at maturity.

Apparently a Chiriquí endemic, but to be looked for also in nearby Costa Rica, especially in the region east of San Vito.

Materials examined. PANAMA. CHIRIQUÍ: Boquete District, Bajo Chorro, rainforest, 6,000 ft., *Davidson 431* (holotype, US; isotypes, F, GH), *392* (F not seen); cloud forest, northeastern ridge leading to Cerro Horqueta, 1,800–1,900 m, *Luteyn 3786* (DUKE, F); Cerro Colorado, cloud forest 50 km N of San Félix on the continental divide, 1,200–1,500 m, *Mori & Dressler 7825* (MO); on trail to Cerro Horqueta, in cloud forest, 6,000–6,500 ft., *Proctor 31935* (LL); mossy forest E of Guadalupe along Río Chiriquí Viejo, about 2 mi. NE of Cerro Punta, ridge of Cerro Respinga, *Wilbur & Teeri 13109* (DUKE); disturbed cloud forest about 8 km W of Cerro Punta, in the vicinity of Las Nubes, 6,100–6,400 ft., *Almeda & Nakai 3536* (CAS, LEA); along old road from Boquete to Cerro Punta on cloud forest trail up to the N slope of Volcan Barú, 1,750–1,900 m, 8°50′N, 82°30′W, *Almeda, de Nevers & McPherson 6166* (CAS, LEA); Distr. Bugaba, Cerro Punta, from STRI house to edge of mountain across the river, 8°52′N, 82°33′W, 2,200 m, *van der Werff & Herrera 6330* (LEA, MO); on path up N slope of Volcan Barú, starting along impassable road formerly linking Boquete and Cerro Punta, 8°50′N, 82°30′W, 1,750–1,900 m, *McPherson 11343* (LEA, MO); vicinity of Cerro Punta, above Guadalupe, forested slopes above STRI cabin, 2,300–2,450 m, *McPherson 9380* (LEA, MO).

DISCUSSION

The several structural peculiarities of *Panamanthus panamensis* outlined above, when taken in aggregate, sharply distinguish it from all other neotropical Loranthaceae. In terms of the inflorescence and associated features, the Australian genus *Atkinsonia* would seem to be the most similar. However, such an affinity could only be remote, as it would be qualified by the strictly terrestrial habit of that genus, and the various primitive features associated with it in the seedling stages at least some of which we can safely extrapolate from those of the closely related *Gaiadendron* (Kuijt, 1963, 1965). Any affinity of this sort, therefore, can only be tenuous.

Unfortunately, nothing is known about the chromosomes of *Panamanthus panamensis*, and it is precisely here that significant information might be expected. The primitive trio of *Atkinsonia*, *Gaiadendron*, and *Nuytsia* shares a basic number of $n = 12$, the chromosomes being very small for Loranthaceae (Barlow & Wiens, 1971); in contrast, the small-flowered neotropical genera of Loranthaceae like *Struthanthus* have $n = 8$, the chromosomes being among the largest known in the angiosperms (Wiens, 1964).

The caducous inflorescence bracts referred to in the above diagnosis have not, as far as I am aware, been mentioned in the literature, and contrast strongly to all other species of *Struthanthus* except two or three species that are clearly not related to *Panamanthus panamensis*, such as *S. leptostachyus* (Kuntze) G. Don. Similarly inconspicuous and caducous bracts are normal in *Gaiadendron*, where they may occasionally become elongated, foliar, and persistent (pers. obs.), and also in *Atkinsonia*, where they are always persistent (Barlow, 1966; Kuijt, 1981).

The pollen of *Panamanthus* is similar especially to that of *Struthanthus oerstedii* Standl. (Feuer & Kuijt, 1985) but lacks distinctive, specialized features. There are no significant similarities with the primitive "*Gaiadendron* trio" of monotypic genera which, however, shows extreme palynological contrasts among its component genera, as between *Nuytsia* and *Atkinsonia* (Feuer & Kuijt, 1980). Thus it appears again that great palynological divergence is compatible with close affinities in some mistletoe groups.

Altitudinal preferences are often consistent within individual genera of neotropical mistletoes. Thus, *Gaiadendron punctatum* tends to be a subpáramo species both in Central America and in its major area, Andean South America (Kuijt, 1989). In contrast, *Struthanthus* has strong preferences for low and middle elevations, nowhere occurring at the elevations noted for *Panamanthus panamensis* (1,200–2,450 m).

In summary, the monotypic generic status here proposed more adequately recognizes the unusual nature of the species. In this respect it might be noted that most accepted genera of small-flowered neotropical Loranthaceae are more weakly separated from each other than *Panamanthus* is from other genera. For example, *Phthirusa* and *Dendropemon* are separable only on the basis of triadic vs. monadic inflorescences, respectively.

The morphological isolation of *Panamanthus* would seem to warrant status as a monotypic genus, however, no matter what its affinities to primitive or other mistletoe genera are. At the same time, if *Panamanthus* is related to *Struthanthus* it may, because of its bisexual flowers and monadic inflorescence, be regarded as significantly more primitive than that genus.

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NOTES ON *SWARTZIA* (LEGUMINOSAE: SWARTZIEAE) PRELIMINARY TO THE FLORA OF THE VENEZUELAN GUAYANA[1]

Rupert C. Barneby[2]

ABSTRACT

Five new species of *Swartzia* (Leguminosae: Swartzieae) recently collected within or at the periphery of the Venezuelan Guayana are described and discussed in terms of relationships and morphology: *S. alato-sericea* Barneby, *S. aymardii* Barneby, *S. oedipus* Barneby, *S. palustris* Barneby, and *S. triptera* Barneby. Figures of *S. oedipus* and *S. triptera* are presented. These descriptions are a prelude to an account of *Swartzia* by R. S. Cowan that will appear in J. A. Steyermark's *Flora of the Venezuelan Guayana*, currently in preparation at the Missouri Botanical Garden.

At the time that Richard S. Cowan, the premier student in this century of the genus *Swartzia*, retired from the Smithsonian Institution and from direct participation in systematic work on neotropical Leguminosae, several collectors were actively exploring the flora of Venezuelan Guayana, and others continue to do so. Cowan saw only a small part of the rich collections of *Swartzia* obtained by the Cerro de la Neblina Expedition (1984–1985), and little or nothing collected subsequently. Many of the more recent collections of *Swartzia* from the Guayana Highland have found their way to the New York Botanical Garden, and incidentally, to the author of this article for identification. With the aid of Cowan's monograph (1967) and supplementary papers, most important of which is his as yet unpublished treatment of the genus for Steyermark's *Flora of the Venezuelan Guayana*, I have been able to name, at least to my own satisfaction, the greater part of this material. It will not surprise anyone familiar with the patterns of narrow endemism in *Swartzia* that along the way I have encountered a number of clearly undescribed taxa. The purpose of this article is to place on record those that have been found in Venezuelan Guayana, and to provide names for use in the forthcoming flora of the region.

Swartzia (sect. et subsect. *Swartzia* ser. *Tounateae*) **alato-sericea** Barneby, sp. nov. TYPE: Brazil. Amazonas: Third Serra da Neblina Expedition, between Tatú and Camp III, 22 Dec. 1965 (fr), *Nilo T. Silva & Umbelino Brazão* in *Maguire 60718* (holotype, INPA; isotypes, K, NY, US).

Proxime ut videtur *S. steyermarkii* Cowan affinis, sed foliolis 6–7(nec 2–3)-jugis subduplo angustioribus (± 2.3–3.3, nec 4–6 cm latis) margine eximie undulatis diversa. A *S. angustifoliola* Schery, quoad foliolorum numerum, ambitum, texturam, colorem necnon marginem undulatam congrua, sed foliolorum rhachi late alata, et a *S. sericea* Vog. distantius rhachi alata et calyce intus glaberrima abstat.

A tree 18 m with trunk 1.5 dm DBH, the young branches and raceme axes densely silky pilosulous with narrowly ascending, basifixed, yellowish hairs, the plurifoliolate leaves except for dorsal side of leaf stalk and pulvinules glabrous, the thinly papyraceous leaflets lustrously olivaceous on upper face, dull pale brown on lower, the racemes arising singly and geminate from annotinous leaf axils. Stipules erect, linear-lanceolate 4–9.5 × 0.4–0.7 mm, deciduous. Leaf stalks 11.5–19 cm, the interfoliolar segments 1–3 cm, each margined with a herbaceous, finely venulose wing 1.5–2 mm wide, and, at insertion of each pair of leaflets, produced in front of the pulvinules into a deltate, sharply mucronate tip; pulvinules 2–2.5 mm; leaflets 13–15 per leaf, the proximal pairs slightly smaller, the rest subequilong, the blade of all leaflets oblong-elliptic from obtuse, at point of insertion minutely cordate base, contracted into an obtuse acumen ± 1–1.5 mm, undulate marginally, the larger blades 7.5–10.5 × 2.3–3.3 cm; midrib canaliculate ven-

[1] Illustrated by Bobbi Angell (NY).

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trally, cariniform dorsally, the numerous and slender secondary nerves widely ascending to anastomosis close within the margin and giving rise to a reticulum of nervules finely prominulous on both faces. Racemes subsessile, 6–14 cm, densely many-flowered; bracts lanceolate 2–2.5 mm, deciduous; pedicels 4.5–6 mm, ebracteolate; calyx sericeous externally, glabrous within, splitting into 4 recurved sepals ± 4.5 mm; petals, androecium, and young gynoecium unknown, but the gynoecium pubescent (giving rise to a pilosulous pod). Pod declined, the silky pilosulous stipe 2.5–3.5 mm, the body plumply ellipsoid, broadly rounded at each end, ± 23–27 × 15 mm, slenderly carinate by the ventral suture, the fleshy valves orange when fresh, atrocastaneous and crumpled when dried, thinly pilosulous overall, dehiscent along both sutures; seeds 2, filling the pod cavity and obliquely truncate where mutually distorted by crowding, the aril ± 10 mm long, the rugulose testa ochraceous, highly lustrous.

Distribution. In lowland forest on terra firme, known only from the base of Serra da Neblina near 0°40′N, 66°20′W, close to the Venezuelan border in Amazonas, Brazil, and expected in adjacent Territorio Federal Amazonas, Venezuela. Ripe fruits December–January.

Until the flower of *S. alato-sericea* is obtained, it cannot positively be asserted to be apetalous; yet habital and other characters of foliage and fruit almost certainly attach the species to the apetalous subser. *Tounateae*. In this context the species resembles the widespread *S. sericea* Vog. in habit, form, and number of leaflets, but differs in broadly winged, not terete leaf stalks, and in sepals glabrous on the inner face. Seemingly closer, at least in the winged leaf stalks, is *S. steyermarkii* Cowan, endemic to Venezuelan Guayana, but this differs in leaflets about half as many and twice as wide (as enumerated in the diagnosis). The leaflets of *S. alato-sericea* closely match the shape, number, and undulate leaflet margin of *S. angustifoliola* Schery, a species localized, so far as presently known, on the upper Río Negro in Venezuela; however, *S. angustifoliola* has leaf stalks stipellate at insertion of leaflet pairs and no trace of wing along the stalk between successive pairs.

Swartzia aymardii Barneby, sp. nov. TYPE: Venezuela. Bolívar: Dtto. Sifontes, a lo largo de la carretera El Paují–Icabarú, 80 km al SW de Sta. Elena de Uairén, 26 Sep. 1986 (fl), *G. Aymard C. 4888* (holotype, PORT).

Swartziae roraimae Sandw. arcte affinis, primo intuitu foliolis dorso praeter costam glaberrimis (nec dense appresse pilosis), ulterius antheris majusculis paucioribus (5, nec 11) ac majoribus (2.5–3, nec 2 mm longis) diversa.

Tree ± 5 m tall, with terete branchlets, the young stems and all axes of inflorescence densely pilose-tomentulose with matted, grayish or brownish, basifixed hairs, the leathery, strongly bicolored leaflets glabrous except for midrib dorsally strigulose on dorsal face, dark olivaceous and highly lustrous above, paler dull beneath, the few-flowered racemes borne in uppermost leaf axils of hornotinous branchlets. Stipules linear-lanceolate 1.6–3 mm, of firm texture, long persistent. Leaf stalks 2–6 cm, shallowly sulcate ventrally, not wing-marginate, the lower of two interpinnal segments 2.2–3 cm, the distal one shorter (or in lowest leaves absent); leaflets (3–)5, the deeply wrinkled and pilosulous pulvinules 3–4 mm, the blades broadly or narrowly elliptic-acuminate from cuneate base, (4.5–)5–10 × 1.5–3.5 cm, the lanceolate acumen 7–10 mm; midrib canaliculate above, cariniform beneath, giving rise to narrow, crowded secondary nerves little differentiated in strength and incurved-ascending at ± 45°, these further generating a close reticulum of veinlets, the whole venation immersed on upper face, bluntly prominulous beneath. Racemes 4–8-flowered, the rachis including short peduncle 6–10 cm; bracts obovate 1.5–2 mm, deciduous; bracteoles 2 at base of pedicel subulate ± 2–2.5 mm; pedicels at anthesis 9–14 mm, a little widened and ancipital distally; flower buds immediately prior to anthesis globose, densely brownish silky-pilosulous; sepals 4, glabrous internally, 10–11 mm; vexillum (caducous) white, flabellate from short claw, ± 12 mm, thinly hirsute dorsally, undulate-crispate at margin; androecium glabrous, the anthers of 5 larger stamens 2.5–3 mm, that of many smaller ones 1–1.5 mm, the connective of all muticous; gynoecium glabrous, the gynophore 8–9 mm, the lunately elliptic ovary in profile 8 × 3 mm, the uncinately recurved style 2.5 mm, obliquely truncate at apex. Fruit unknown.

Distribution. In brush savanna at 750 m, known only from the type locality in the northern foothills of Sierra de Pacaraima in southeastern Bolívar, Venezuela. Flowering September–October.

In foliage and inflorescence *S. aymardii* closely resembles *S. roraimae* Sandw., as yet known only from the southwestern escarpment of Mt. Roraima (*im Thurn 67*, K = NY Neg. *940*), but is different in dorsally glabrous, not densely appressed-pilose

leaflets. Further differences are fewer (5 vs. 11) large anthers 2.5–3 (vs. 2) mm long, and slightly shorter stipules and bracts, characters that will deserve close scrutiny when more collections of each species become available. *Swartzia roraimae* was found by im Thurn at 1,500 m, an elevation unusually high for the genus, and *S. aymardii* at 750 m, suggesting ecological differentiation.

Swartzia (sect. et ser. *Possira*) **oedipus** Barneby, sp. nov. TYPE: Brazil. Amazonas: Mun. Cucuí, in terra firme forest on Rio Xié, 1 hour by motorboat upstream from confluence with Rio Negro (0°58′N, 67°10′W), 25 Oct. 1987 (young fr), *D. C. Daly* (with *P. J. M. Maas, C. F. Sá & R. P. Lima*) *5490* (holotype, INPA *150988*; isotypes, F, MO, K, NY, US). Figure 1.

Foliorum rachi exalata foliolisque parvis (5 cm usque longis) praeter costam glabris cum *S. foliolosa* Cowan, *S. brachyrrhachide* Harms et *S. longistipitata* Ducke comparabilis, ultimae verisimiliter proxime affinis, a prima foliolis dimidio minoribus necnon pedicellis cum calycis segmentis extus dense sericeis (nec glabris), a secunda et tertia foliolis 4–5(nec 1–3)-jugis, ab omnibus pedicellis calycem versus incrassatis et 2 mm usque crassis diversa.

Trees attaining 20 m with trunk 2 dm DBH, the annotinous and older branchlets ashen glabrate, the hornotinous ones together with terete leaf rachises, petiolules, and dorsal costa of leaflets gray silky-strigulose, the foliage bicolored, the leaflets glossy dark green above, paler dull beneath, the densely brownish sericeous few-flowered racemes axillary to 1–3 distal leaves of each new branchlet, the furthest pseudoterminal, all shorter than the subtending leaf. Stipules linear-attenuate 2.5–5 mm, caducous. Leaf stalks 4–6.5 cm, the petiole proper and the interfoliolar segments 8–13 mm; petiolules 2–2.5 mm, the stipels subobsolete; leaflets 9–11, varying in outline from narrowly ovate- to lance-acuminate from rounded base, including the apically emarginate acumen (5–6 mm) 35–50 × 14–18 mm, the costa shallowly impressed above, cariniform beneath, giving rise to many crowded, incurved-ascending secondary veins and a finer reticulum, all prominulous on both faces of blade. Racemes 3–5-flowered, the axis including short peduncle 3–4 cm; bract and bracteoles at base of each pedicel narrowly triangular 1.5–2 mm, deciduous; pedicels stout, 8–12 mm, clavately thickened upward, at apex ± 2 mm diam.; sepals 8–10 mm, densely silky externally, glabrous within; petal and complete androecium not seen, the anther of shorter stamens ± 0.6 mm, glabrous; ovary glabrous; style subulate, gently incurved, ± 3 mm, the stigma poriform; stipe of immature fruit 10–14 mm.

Distribution. In lowland, noninundated forest. Known only from the upper Río Negro basin astride the Venezuela–Brazil frontier near Piedra de Cucuy in Territorio Federal Amazonas, Venezuela, and adjacent state of Amazonas, Brazil. Flowering ± September–October.

Additional material examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: margem esq. do Río Negro no caminho para Pedra de Cucui (1°15′N, 66°51′W), 28 Oct. 1987 (immature fr), *W. A. Rodrigues 10795* (F, GH, K, MO, NY, US).

Swartzia oedipus has the essential characters of section and series *Possira* and falls within the circle of affinity defined by couplets 14–20 in Cowan's (1967: 26) key to that group. Leaflets glabrous beneath except for strigulose costa make it most nearly comparable to *S. foliolosa* Cowan (of southeastern Colombia), to the somewhat polymorphic and widely dispersed *S. brachyrrhachis* Harms, and to *S. longistipitata* Ducke (local in central Brazilian Amazonia), which may be its closest known ally. It differs from *S. foliolosa*, as described by Cowan (1967: 190), in leaflets only half as large and in densely brownish sericeous (vs. glabrous) axes of inflorescence, from *S. brachyrrhachis* in having 8–11 (vs. 1–5) leaflets per leaf, and from *S. longistipitata* by leaflet number (8–11 vs. 3–7 per leaf) and by sepals glabrous (not thinly silky) internally. It differs from all of these in the stout pedicels clavately enlarged upward and about 2 (vs. 1 or <1) mm diam. at apex, the character that suggested the epithet *oedipus*. The small glossy leaflets, the contrast between gray indumentum of stem and leaf stalk and brownish silky indumentum of inflorescence, and the perfectly glabrous, long-stipitate gynoecium are characteristic features.

Swartzia palustris Barneby, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: hills 2.5 km SW of Base Camp, 400–500 m, SW side of Cerro de la Neblina (00°49′N, 66°10′W), 20 Feb. 1985 (fl, fr), *M. Nee 30979* (holotype, VEN; isotype, NY).

Inflorescentia e ramulorum coaevorum axillis orta, pedicellis ebracteolatis, styloque laterali brevissimo sect. *Swartziae* subsect. *Swartziae* referenda, serie autem inter *Pittierianis* et *Racemosis* ambigua, cum illa bracteolarum defectu, cum hac foliis unifoliolatis congrua, sed foliolis solitariis inferne aureo-strigosis in utraque serie anomala, affinitatis verae petendae.

Slender trees 3–15 m tall with sometimes sarmentose branches, the annotinous branches gla-

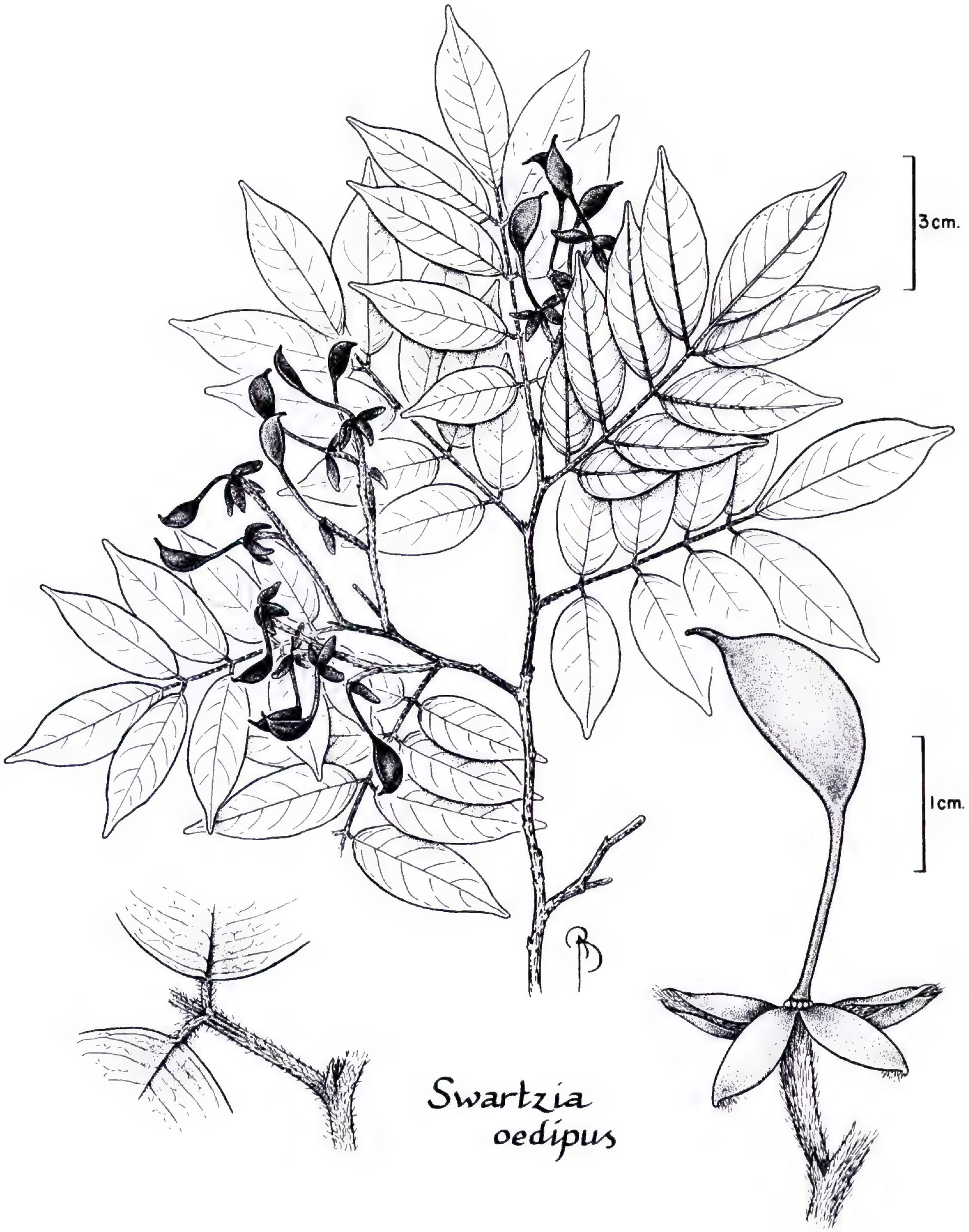

FIGURE 1. *Swartzia oedipus* Barneby. Center, branchlet just after anthesis; lower left, stipule and base of leaf stalk; lower right, gynoecium from branchlet, enlarged. (All from *Daly 5490.*)

brate, the young ones, the lower face of leaflets, and the whole inflorescence densely golden sericeous with contiguous and parallel, forwardly appressed hairs, the leaves unifoliolate, the chartaceous leaflet olivaceous, glabrous, and lustrously reticulate above, the short racemes arising singly or 2–3 together from hornotinous leaf axils. Stipules (few seen) triangular-subulate, less than 1 mm, fugacious. Leaf stalks terete, including the pulvinus 5–13 mm, at middle 0.7–1 mm diam.; stipels 0;

pulvinule of solitary leaflet 2.5–5 mm; leaflet broadly elliptic from rounded or broadly flabellate base, contracted into a slender, apically emarginate acumen ± 1–2 cm, the blade including acumen 7.5–15 × 3.5–8 cm; venation pinnate, the midrib shallowly sulcate ventrally, cariniform dorsally, giving rise on each side to 7–9 major secondary nerves incurved-ascending to anastomosis shortly within the plane margin and to many weaker intercalary ones, these all generating a reticulum of nervules finely prominulous on both faces. Primary axis of racemes 4–12 cm; bracts ovate, scarcely 1 mm; bracteoles 0; pedicels 5–9 mm, a little compressed but not thickened upward; flower buds just prior to anthesis globose, 4–5 mm diam., densely golden sericeous; sepals 4, ± 4.5 mm, glabrous internally; vexillum ± 6 mm diam., thinly pilose dorsally, caducous; androecium glabrous, the anther of the ± 104–114 smaller stamens 0.7–1 mm, that of 3 stout abaxial ones 2.2–2.7 mm, arched backward, apiculate; gynoecium glabrous, the gynophore at anthesis 3–4 mm, the lunate ovary 3–3.5 × 1.6–1.9 mm, incurved and contracted into an almost obsolete style, the stigma poriform. Pod obliquely oblong- or obovoid-ellipsoid, cuneately contracted into a stipe 4–8 mm, the body in profile (26–)30–34 × 15–21 mm, the style base becoming infra-apical, the ripe valves orange, when dried crustaceous brittle, dull cinnamon brown; seed solitary, the fimbriate aril ± 15–17 × 17–20 mm, the body narrowly reniform ± 25 × 9–11 mm, the testa castaneous lustrous.

Distribution. In swampy forest with *Mauritia* and in rainforest on low hills, 130–400 m, known only from the headwaters of ríos Baria–Mawarinuma at 0°50–53′N, 66°10′W, near SW foot of Cerro de la Neblina, Territorio Federal Amazonas, Venezuela. Flowering July, January–March.

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS, all from the vicinity of the type locality: 30 Mar. 1984 (fr), *R. Liesner 17035* (MO, NY); 20 Apr. 1984 (fr), *W. W. Thomas 3162* (NY); 8 May 1984 (fr), *W. W. Thomas 3411* (NY); 27 Nov. 1984 (fr + young fl buds), *D. Bell 328* (NY); 27 Jan. 1985 (fl), *M. Nee 30564* (NY); 16 Feb. 1985 (fr), *Boom & Weitzman 5873* (NY).

Swartzia palustris neatly fits Cowan's (1967: 13, 18) definition of sect. *Swartzia* subsect. *Swartzia*, but is not easily assimilated into any series of the subsection. The combination of glabrous gynoecium and absence of bracteoles leads directly to the small group *Pittierianae*, but these have regularly 2–4-jugate, almost glabrous leaves, and consequently a facies very different from *S. palustris*, notable for unifoliolate leaves clothed beneath with a dense indumentum of appressed golden hairs. If its lack of bracteoles be disregarded, *S. palustris* would be compatible with the character of series *Racemosae*, where it finds a superficial resemblance in *S. racemosa* Benth. This last differs greatly, however, in very short leaf stalks composed entirely of pulvinus and terminal pulvinule, in lack of golden indumentum, in conspicuous development of stipules, floral bracts and bracteoles, and in almost glabrous (not golden silky) flower buds and a distinctly developed style. The true relationship of *S. palustris* is unknown.

Swartzia triptera Barneby, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Río Negro, in lowland tropical evergreen forest, 140 m, Base Camp on S side of Río Baria (= Mawarinuma), SW side of Cerro de la Neblina, 00°49′30″N, 66°06′20″W, 13 Feb. 1985 (fr), *M. Nee 30839* (holotype, VEN; isotype, NY). Figure 2.

Bracteolarum defectu styloque obliquo brevissimo sect. *Swartziae* subsect. *Swartziae* referenda, foliorum rachi tereti estipellata et gynoecio parcissime puberulo melius cum ser. *Benthamianis* Cowan congrua, sed inter has legumine secus suturas seminiferam late 2- et abaxialem 1-alato (alis 3.5–7 mm latis) insignis.

Trees 4–12 m with smooth fuscous branchlets, glabrous up to the thinly minutely silky strigulose inflorescence, the ample leaflets subconcolorous, dull olivaceous or on lower face dull brown-olivaceous, the racemes of small flowers borne singly or 2–3 together in the axil of coeval leaves. Stipules lacking. Leaf stalks 1–2.9 dm, terete, estipellate; leaflets in all but an occasional depauperate leaf either 5 or 7, the cylindric black wrinkled pulvinules 6–14 × 1.1–1.6 mm; leaflets ovate or elliptic-ovate from broadly cuneate or flabellate base, abruptly contracted distally into a caudiform acumen 1–1.5 cm, the blade of lateral ones 10–19 × (3–)4–6.5 cm, that of the stalked terminal one 13–20 × (4–)5–9.5 cm; midrib impressed above, cariniform beneath, giving rise to 5–6 pairs of slender major secondary nerves incurved-ascending to anastomosis well within the plane, finely corneous margin, the intervenium of both faces reticulate with a mesh of incised veinlets. Racemes ascending, ± 10–25-flowered, the axis including peduncle (7–)10–24 cm; bracts subulate 1.5–3 mm, deciduous after anthesis; bracteoles 0; pedicels at anthesis 4–5 mm, in fruit 5–12 mm; flower buds prior to anthesis obnapiform, bluntly pentagonal above middle, thinly puberulent; sepals 5, sharply reflexed, lance-ovate 6–7 mm, glabrous internally; vexillum membranous white glabrous,

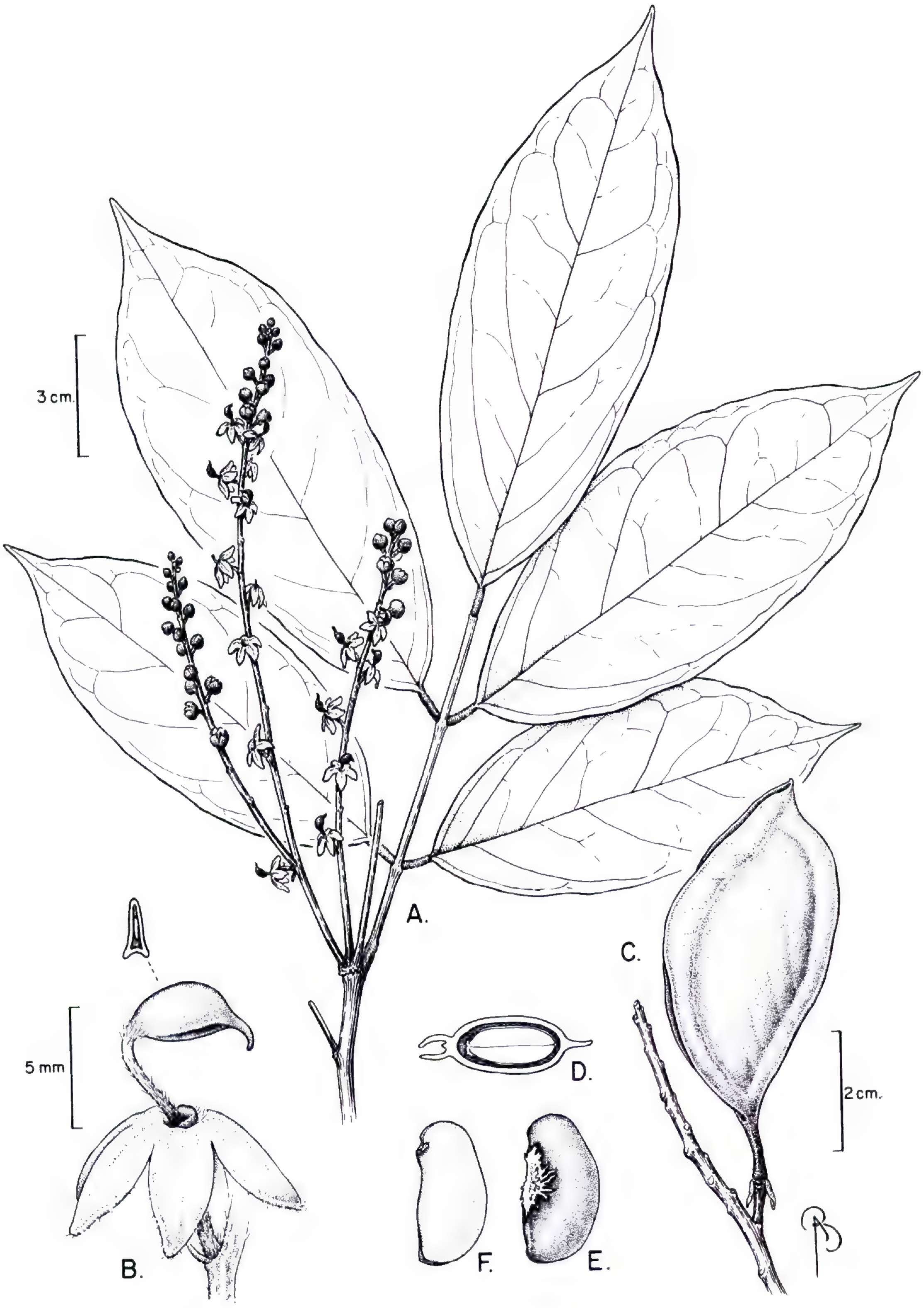

FIGURE 2. *Swartzia triptera* Barneby.—A. Leaf and inflorescence.—B. Calyx and ovary.—C. Pod.—D. Cross section of pod.—E. Seed.—F. Seed testa. (A, B from *Davidse 27068*; C–F from *Nee 30839*.)

caducous with the androecium as the calyx expands, in outline ovate beyond the short claw, ± 7 × 4 mm; androecium glabrous, the filaments yellow, the ± 70 small anthers 0.6–0.7 mm diam., the 4 large ones 1.5 mm; gynophore 2.5–2.8 mm, puberulent; ovary ± 3 mm, glabrous except for a few hairs at base and along sutures; style obliquely terminal ± 1 mm, incurved, the stigma punctiform. Pod ascending, stipitate, the stipe 7–11 mm, the body in profile asymmetrically elliptic 5.5–8 × 2.7–3 cm, cuneately attenuate at base, more abruptly contracted at apex into a short triangular beak, laterally compressed but turgid over the 2 seeds, girdled lengthwise by wings 3.5–7 mm wide arising 2 from the adaxial and one from the abaxial suture, the stiffly leathery valves glabrous, vertically shallow-grooved over the convex fertile seed chamber, this in transverse section ± 18–20 × 9–10 mm; exocarp smooth papery fuscous, the endocarp crustaceous 0.6 mm thick; seeds ± 20 × 11 × 10 mm, the fimbriate aril 4–5 mm diam., the fragile papery testa lustrously castaneous.

Distribution. In terra firme forest at ± 140 m, known only from the SW base of Cerro de la Neblina in Territorio Federal Amazonas, Venezuela. Flowering July–August; fruits ripe November–February.

Additional specimens examined. All from the immediate vicinity of Cerro de la Neblina Base Camp on Río Mawarinuma: 6–7 July 1984 (fl), *G. Davidse & J. S. Miller 27068* (NY); 6 July 1984 (in bud), *J. S. Miller 1735* (NY); 27 Nov. 1984 (fr), *Boom & Weitzman 5165* (NY); 1 Feb. 1985 (fr), *Boom & Weitzman 5476*; 7 Feb. 1985 (sterile), *Boom & Weitzman 5660.*

By virtue of habit, terete estipellate leaf stalks, absence of bracteoles, and almost glabrous gynoecium with very short incurved style, *S. triptera* appears related to ser. *Benthamianae* Cowan of subsect. *Swartzia*, where it closely resembles, when flowering or sterile, *S. benthamiana* Miquel and *S. laevicarpa* Amshoff. The fruit is nearly that of the latter as to size and outline, but unlike that of any described species of the genus is doubly winged along the ventral and singly so along the dorsal suture. The ripe fruit is strangely similar in structure to that of the African *Erythrina greenwayi* Verdcourt and has no precedent in *Swartzia.*

Literature Cited

Cowan, R. S. 1967. Flora Neotropica Monograph No. 1. *Swartzia* (Leguminosae, Caesalpinioideae, Swartzieae). Hafner Publishing, New York.

CYRTOCARPA KUNTH (ANACARDIACEAE) IN SOUTH AMERICA[1]

John D. Mitchell[2] *and*
Douglas C. Daly[2]

Abstract

Cyrtocarpa has previously been known only from Baja California and western Mexico; here we report two species of the genus from South America. *Cyrtocarpa velutinifolia* (Cowan) Mitchell & Daly, presented here as a new combination, was originally published as a *Bursera* and later transferred to *Tapirira* (Anacardiaceae). The Anacardiaceae and Burseraceae show frequent morphological convergence in the drier tropics; moreover, in several genera they display strong similarities in staminate flower structure. *Cyrtocarpa velutinifolia* occurs in savannas and granitic outcrops in Colombia, Venezuela, Brazil, and Guyana. *Cyrtocarpa caatingae* Mitchell & Daly, a new species represented by four collections from the dry thorn-scrub vegetation of Bahia, Brazil, resembles the Mexican *C. procera* Kunth and appears to be most closely related to it.

Cyrtocarpa Kunth is a genus heretofore known from two Mexican species, *C. procera* Kunth and *C. edulis* (Brandegee) Standl. Now, two additional species are recognized in South America. One of them was originally described in the Burseraceae; the other was discovered recently in collections from Bahia, Brazil.

The Burseraceae and Anacardiaceae are accepted as being closely related by most contemporary authors (e.g., Cronquist, 1981; Takhtajan, 1980; Thorne, 1976). The two families show considerable morphological convergence in dry tropical habitats, where species of both families display a densely branched, tortuous habit; succulent branchlets; leaves that are imparipinnate, congested toward the branchlet apices, and deciduous; and drupaceous fruits (eventually dehiscent in Burseraceae). For example, *Bursera microphylla* A. Gray and *Pachycormis discolor* (Benth.) Coville are sympatric in Baja California and are very similar in appearance (pers. obs.). In arid portions of East Africa, some species of *Commiphora* Jacq. (Burseraceae) and *Lannea* A. Rich. (Anacardiaceae) are difficult to distinguish (J. B. Gillett, pers. comm.). In southern Africa, some species of *Commiphora* and *Rhus* L. show a strong resemblance.

The occasional similarities in the structures of the staminate flowers of these two families led Cowan (1952) to describe an anacardiaceous plant from Guyana as *Bursera velutinifolia*. This species has since been collected in Brazil, Colombia, and Venezuela (Fig. 1). In the staminate flowers, the only characters that place the species out of the Burseraceae are the imbricate (induplicate-valvate in *Bursera*) petals and the pistillode that is 3–5-lobed from the base (always 3-lobed in *Bursera*). The deciduous habit of this species is also characteristic of *Bursera*.

After examining pistillate flowers, Marcano-Berti (1986) transferred *B. velutinifolia* to *Tapirira* Aublet (Anacardiaceae). This transfer to Anacardiaceae is supported by the solitary, apotropous ovules, apically suspended within the locules (vs. two epitropous, laterally attached ovules in Burseraceae); carpels more than three (2–3 in *Bursera*); and mesocarp and endocarp distinct. Moreover, the styles become separated in the developing fruit, whereas in all Burseraceae there is a single, occasionally branched style. We agree with the implication of Marcano-Berti's transfer that the species belongs in the tribe Spondiadeae (Engler, 1882) because of its apically suspended ovules and the ovary with usually more than three carpels. Its affinity with the Spondiadeae was recognized by the indigenous population in Venezuela: it is called "jobillo," and the common name for *Spondias* is "jobo." However, examination of the available material has brought to light several fundamental

[1] We thank J. A. Kallunki, S. A. Mori, and W. W. Thomas for critically reading the manuscript; D. W. Stevenson for enlightening comments on fruit morphology; R. P. Barneby for assistance with the Latin diagnosis; B. Angell for the revealing illustrations; and A. Kostermans, P. Berry, and one anonymous reviewer for editorial assistance. We are also grateful to the staffs of the following herbaria for the loan of specimens: F, K, MO, P, PORT, VEN. The Fund for Neotropical Plant Research of the New York Botanical Garden covered some expenses associated with the production of this manuscript.

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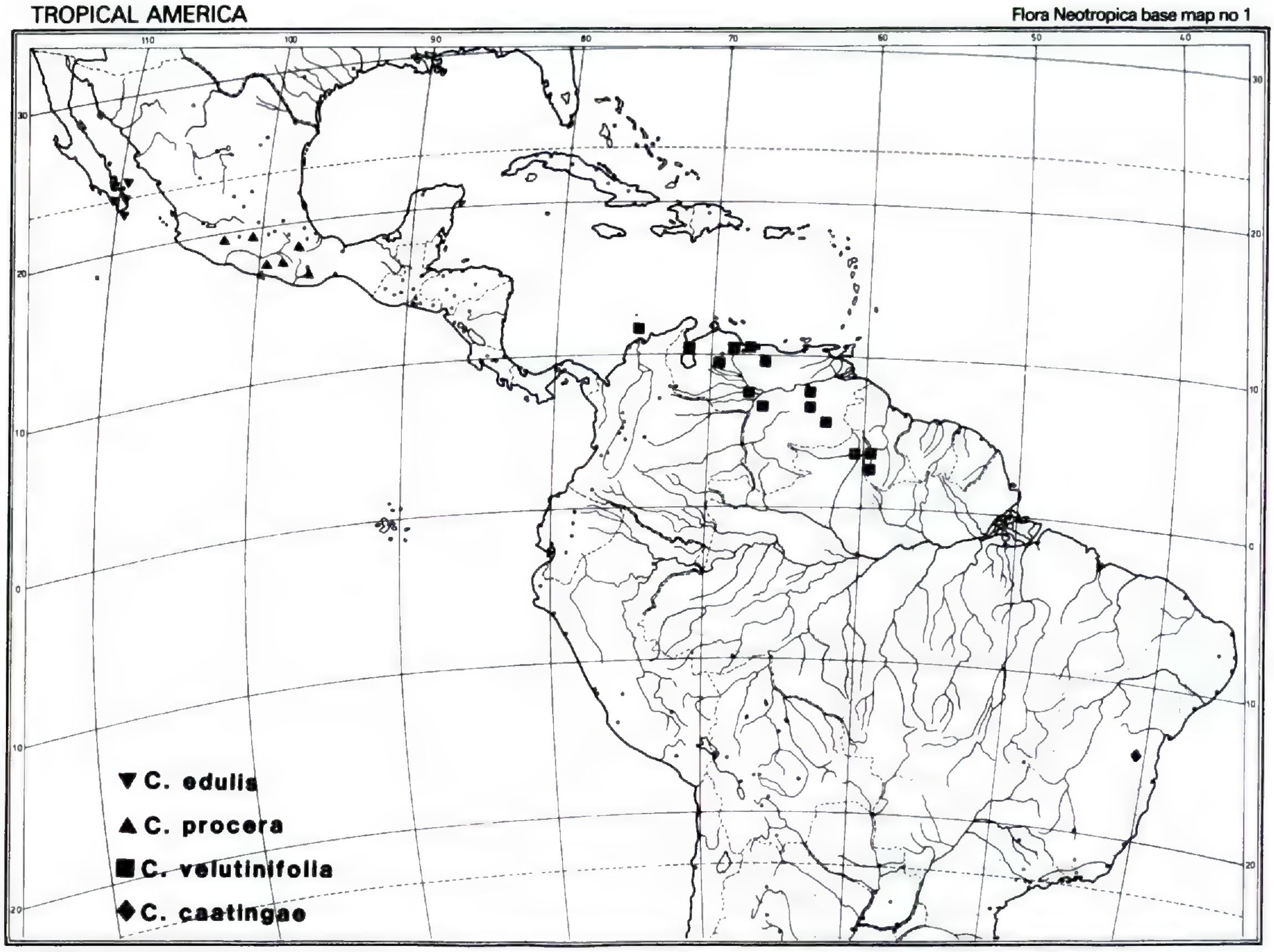

FIGURE 1. Distribution of *Cyrtocarpa* species. This map is Flora Neotropica base map no. 1, published by the State University of Utrecht, The Netherlands.

characters that preclude its placement in *Tapirira* and necessitate its transfer to *Cyrtocarpa*. These characters are summarized in Table 1.

Since we have reexamined *Cyrtocarpa*, we present below a key to the neotropical genera of Spondiadeae, a description of *Cyrtocarpa*, and a key to the species of the genus; one new combination is made and a new species is described.

KEY TO THE NEOTROPICAL GENERA OF SPONDIADEAE

1a. Leaflets with intramarginal vein; stone consisting of bony endocarp enclosed in a fibrous matrix ..... *Spondias*

1b. Leaflets without intramarginal vein; stone cartilaginous or bony, fibrous matrix lacking.

2a. Plants deciduous; leaves congested at branch apices; pistil(lode) glabrous, stone with one or more opercula (lids).

3a. Buttresses present; in pistillate flowers, all locules containing an ovule; stone depressed-globose, pentagonal or turbinate; opercula 5–6; seeds usually 5–6; moist forests ..... *Antrocaryon*

3b. Buttresses absent; in pistillate flowers, only one locule containing an ovule; stone slightly oblique-oblong, obovoid, or ovoid; opercula 1–5; seed 1; dry forests, savannas, and thorn scrub ..... *Cyrtocarpa*

2b. Plants evergreen; leaves not congested at branch apices; pistil(lode) pubescent; stone without opercula ..... *Tapirira*

Cyrtocarpa Kunth in HBK, Nov. Gen. et Sp. 7: 20, t. 609. 1824. TYPE: *Cyrtocarpa procera*.

Dasycarya Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1853: 98. 1854. TYPE: *Dasycarya mexicana*.

Small to medium-sized polygamodioecious trees of dry to arid habitats, branchlets somewhat succulent (drying wrinkled), resin apparently nonallergenic. *Leaves* deciduous, congested toward the branchlet apices, imparipinnate; lateral leaflets sessile or short-petiolulate, margin entire, densely pubescent on both surfaces, venation eucamptodromous. *Inflorescences* subterminal, paniculate (pseudospicate in *C. velutinifolia*), initiated in leafless condition. Flowers 5-merous, aestivation imbricate; petals patent at anthesis; diplostemonous; disk intrastaminal, annular, crenulate, fleshy; pis-

TABLE 1. Comparison of *Tapirira*, *Cyrtocarpa velutinifolia*, and *Cyrtocarpa*.

Character	*Tapirira*	*Cyrtocarpa velutinifolia*	*Cyrtocarpa*
Leaves			
Phenology	evergreen	deciduous	deciduous
Leaflets	petiolulate	subsessile	subsessile
Venation	usually brochidodromous	eucamptodromous	eucamptodromous
Indumentum	along veins	all of surface	all of surface
Flowers			
Pistil(lode)	pubescent	glabrous	glabrous
Ovary	1-locular	1–3(–4)-locular	2–5-locular*
Fruit			
Shape	subsymmetric	oblique	oblique
Stone	usually cartilaginous	bony	bony
Operculum	absent	present (1)	present (2–5)

* Engler (1882) misinterpreted the ovary of *Cyrtocarpa* as 1–2-locular.

tillode consisting of five styllodes; pistil doliform, styles separate, glabrous or papillate (vs. densely pubescent in *Tapirira*), ovary 1–5-locular. *Fruit* a drupe, purple or yellow to orange at maturity, obliquely obtuse-oblong, styles often persistent, surface often pubescent (vs. glabrous in *Spondias*), exocarp thin, mesocarp fleshy, endocarp bony, with 1–5 opercula; seeds apparently 1, testa with saddle-shaped patch corresponding to the hilum, cotyledons reniform.

KEY TO THE SPECIES OF *CYRTOCARPA*

1a. Secondary axes of inflorescence pseudospicate ..... *C. velutinifolia*
1b. Secondary axes of inflorescence paniculate.
  2a. Lateral leaflets broadly elliptic to broadly (ob)ovate; anther connective not glandular-mucronulate; flowers 8 mm diam. ..... *C. edulis*
  2b. Lateral leaflets lanceolate to narrowly elliptic; anther connective glandular-mucronulate; flowers 4–6 mm diam.
    3a. Ovary 2–5-locular; upper leaflets frequently alternate; filaments 1.8–2 mm long, anthers 1 mm long; pistillode not exceeding disk; western Mexico ..... *C. procera*
    3b. Ovary 1-locular; upper leaflets always opposite; filaments 1.3–1.5 mm long, anthers 0.5 mm long; pistillode exceeding disk; Bahia, Brazil .. *C. caatingae*

Cyrtocarpa velutinifolia (Cowan) Mitchell & Daly, comb. nov. *Bursera velutinifolia* Cowan, Brittonia 7: 401–402. 1952. *Tapirira velutinifolia* Marcano-Berti, Pittieria 13: 23. 1986. TYPE: Guyana: Sand Creek, Rupununi River, Sep. 1948, *Wilson-Browne 112* (*F.D. 5650*) (holotype, NY). Figures 1, 2.

Loxopterygium gutierrezii Barkley, Lloydia 25: 121–122. 1962. TYPE: Colombia. Magdalena: 200 m alt. near Masinga, near Santa Marta, 22 Jan. 1899, *H. H. Smith 911* (holotype, NY; isotypes, A, BM, F, K, MICH, US).

The principal characters that have been used to separate genera in the Spondiadeae are the leaf venation; number of carpels; number of styles; degree of fusion of the styles; number of locules; structure of the mesocarp; presence or absence of opercula in the stone; other characters of the endocarp; and number of seeds developing per fruit (Engler, 1882; Hill, 1933, 1937; Kostermans, 1981; von Teichman, 1987; von Teichman & Robbertse, 1986; von Teichman & van Wyk, 1988; Wannan, 1986). The generic limits in the Spondiadeae are not clear in many cases, but there are consistent qualitative characters that can be used to distinguish *Tapirira* and *Cyrtocarpa*.

Tapirira is characterized by evergreen leaves; petiolulate lateral leaflets, usually with brochidodromous venation; densely pubescent pistil and pistillode; consistently unilocular ovary; subsymmetric fruit; and inoperculate stone. In contrast, *Cyrtocarpa* has deciduous leaves; (sub)sessile lateral leaflets with eucamptodromous venation; glabrous pistil and pistillode; 1–5-locular ovary; oblique fruit; and operculate stone.

Bursera velutinifolia possesses all the characters of *Cyrtocarpa*. Removal of the exocarp and mesocarp from fruits of *Boom & Eisenberg 6056* (MO, NY) and of *Aristiguieta 6090* (MO, NY) revealed a single operculum, located subapically on the anterior face of the stone (see Fig. 2). The genus most closely related to *Cyrtocarpa*, *Operculicarya* H. Perrier from Madagascar, also has

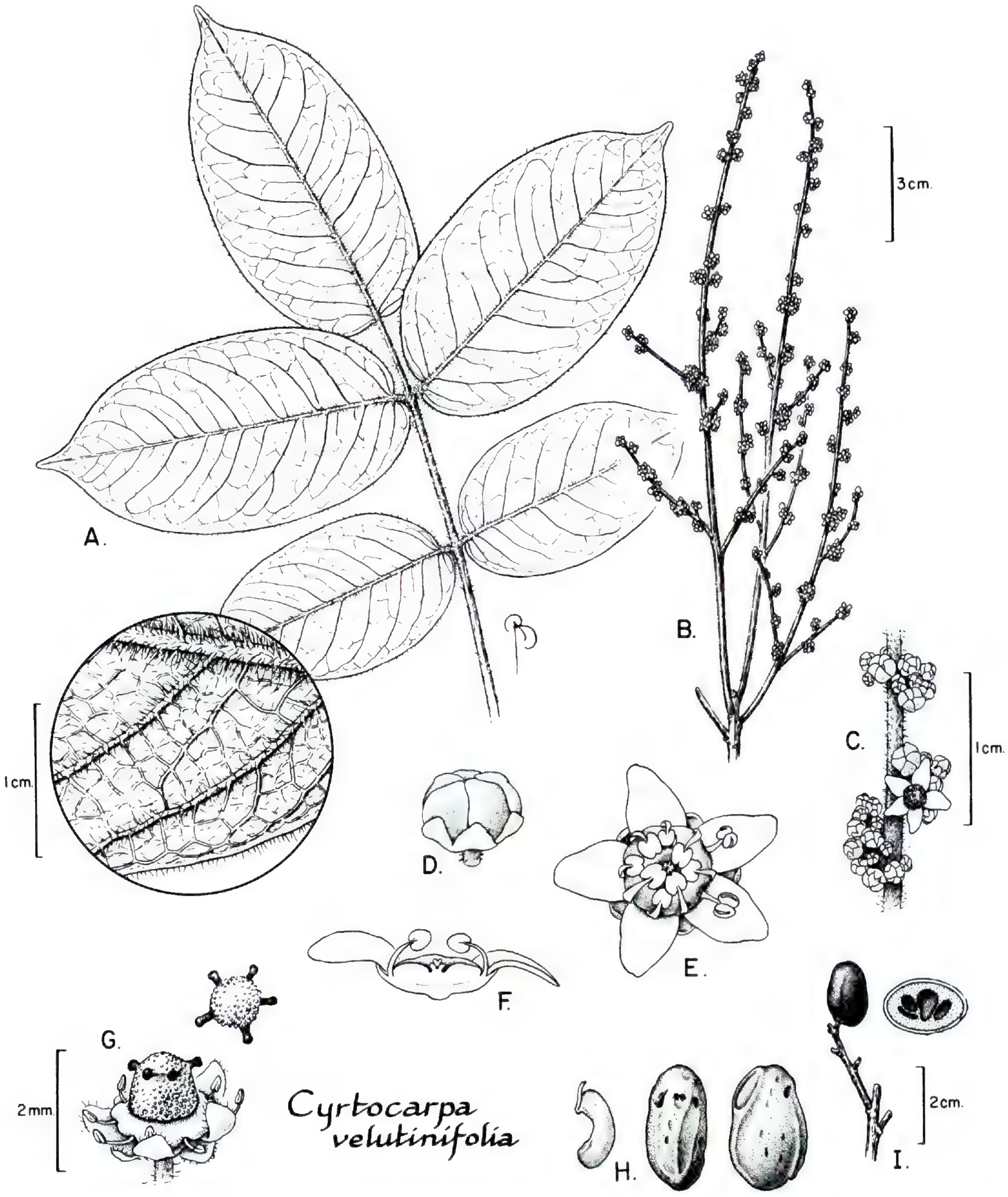

FIGURE 2. *Cyrtocarpa velutinifolia* (Cowan) Mitchell & Daly.—A. Part of mature leaf, including detail of abaxial leaflet surface.—B. Staminate inflorescence, showing pseudospicate structure.—C. Detail of staminate inflorescence, showing reduced tertiary axes.—D. Bud.—E. Top view of staminate flower.—F. Longisection of staminate flower, showing pistillode not exceeding disk.—G. Pistillate flower, post-anthesis, including top view of pistil.—H. Embryo; dorsiventral and lateral views of stone, showing operculum.—I. Portion of infructescence; transsection of drupe. Based on *Bunting 4777* (A), *Goodland 1046* (B, C), *Wilson-Browne 518* (*F.D. 5919*) (D–F), *Wingfield 1011* (G, I), and *Aristiguieta 6090* (H).

unioperculate stones, but it is evergreen and has horseshoe-shaped (vs. reniform) cotyledons and usually five stamens.

The operculum of the stone is a structure associated with a specialized germination mechanism (Hill, 1933, 1937). It functions as a door in the protective woody tissue of the stone through which the seed germinates. In the Anacardiaceae, operculate stones are restricted to 10 of the 18 genera in the tribe Spondiadeae.

Additional specimens examined. VENEZUELA. APURE: Distrito Pedro Camejo, Piedra de San Vicente, 9 airline km N of Puerto Paez; 6°18′N, 67°27′W, 80–160 m, 26 Feb. 1978, *Davidse & A. González 14581* (VEN). ARAGUA: Parque Nacional Henri Pittier, near limit of El Piñal (N of Maracay), at foot of cerro, 500–600 m, 12 May 1972, *Bunting 4777* (NY). BOLÍVAR: Parque Caroní, Sep. 1965, *Aristiguieta 5877* (NY); Distrito Cedeño, valley of Caño Colorado, vic. of Panare Indian village, 30 km SW of National Guard post Maniapure, ca. 200 m, 6°45′N, 66°37′W, 5–7 Apr. 1985, *Boom & Eisenberg 6056* (K, MO, NY); Represa Guri, ca. 55 km NE of Ciudad Piar, elev. 250–300 m, ca. 7°35′N, 63°07′W, 4–5 Apr. 1981, *Liesner & González 11243* (MO, NY); upstream on Rio Asa from Raudal Cotúa, 2 Aug. 1960, *Steyermark 86814* (NY); northernmost slopes of Cerro Baraguán, 100–330 m, 13 Jan. 1956, *Wurdack & Monachino 41240* (NY). CARABOBO: vic. of Valencia, 400–800 m, Dec. 1919, *Pittier 8679* (NY). FALCON: Distrito Democracia, Pueblo Nuevo, 20 km S of Urumaco, 520 m, 24 June 1982, *R. Wingfield 1011* (K). GUARICO: forests of Tamanaco, Altagracia de Orituco–Chaguaramas, May 1966, *Aristiguieta 6090* (NY); near Paso Real, June 1966, *Aristiguieta 6165* (NY). PORTUGUESA: Distrito Guanare, Mesa de Cavacas, property of UNELLEZ, 200 m, 9°04′N, 69°49′W, 5 Sep. 1988, *Aymard & Cuello 7024* (NY, PORT). ZULIA: Distrito Miranda, vic. of El Consejo de Ciruma, near spring of El Cardón, 150–200 m, 7 Aug. 1979, *Bunting 7872* (NY). GUYANA: Rupununi northern savanna, Moreru [Moreiro], 21 Oct. 1963, *Goodland 1046* (NY); Iramaipang, Kanuku Mts., *Wilson-Browne 518* (*F.D. 5919*) (NY). BRAZIL. RORAIMA: Rio Uraricoera, Cachoeira Urubu, 18 Nov. 1979, *Pires et al. 16709* (NY).

Cyrtocarpa caatingae Mitchell & Daly, sp. nov. TYPE: Brazil. Bahia: Mun. Manoel Vitorino, 1–5 km W of Manoel Vitorino on road to Catingal, 20 Nov. 1978, *S. A. Mori, T. S. Santos & C. B. Thompson 11248* (holotype, CEPEC; isotypes, ILL, K, NY, RB). Figures 1, 3.

Cyrtocarpae procerae ob inflorescentiam paniculatam, foliola lanceolata vel anguste elliptica, et connectivum antheridii glanduloso-mucronulatum similis et affinis; ab eo autem ob ovarium uniloculare (nec 2–5-loculare), stamina breviora, et pistillodium discum superans differt.

Deciduous, dioecious shrub or small tree ca. 3.5 m tall. Branch apices somewhat fleshy (drying wrinkled). Leaves (only immature ones known) flushing at time of flowering, congested near the apices, 3–5-jugate; leaflets lanceolate to narrowly elliptic, lateral ones subsessile with truncate and slightly oblique base, terminal ones petiolulate with acute base, apex obtuse and apiculate, venation eucamptodromous, leaf surfaces sericeous, with dense, ascending trichomes 0.2–0.4 mm long. Inflorescences subterminal, paniculate, 6–11.7 cm long, peduncle ca. 2.5–3 cm long, secondary axes 0.5–2 cm long, tertiary axes 1.5–6 mm long, pedicels 1.5–2 mm (staminate flowers) and 2–2.5 mm (pistillate) long. Flowers greenish, 5-merous and diplostemonous, 4 mm diam.; calyx teeth semicircular, fleshy, 1 × 0.7 mm, pubescence as on inflorescences, margin ciliate; petals oblong, 2–2.4 × 1 mm, glabrous, veins arcuate and branching. Staminate flowers with filaments 1.5 mm (antepetalous) and 2 mm (antesepalous) long, anthers broadly elliptic, 0.6 mm long, connective glandular-mucronulate, apiculum drying black; disk thin; pistillode consisting of 3–5 stylodes, each 0.6 mm long, greatly exceeding disk. Pistillate flowers with filaments 1.5 and 2 mm long, anthers in dorsiventral view lanceolate, 0.4–0.5 mm long; pistil doliform with rounded apex, 1–1.5 mm × 0.7–1 mm, glabrous, styles 5, 0.2–0.25 mm long, separate, spreading, stigmas discoid; locule 1, ovule 1, pendent. Developing fruit obliquely oblong, apex obtuse, styles persistent, mature fruit unknown.

Paratypes. BRAZIL. s.l., 1816–1821, *Saint-Hilaire s.n.* (P). BAHIA: Igreja Velha, 1841, *Blanchet 3418* (NY; P—2 sheets); caatinga near Caldeirão, Oct. 1906, *Ule 7256* (K).

Distribution. Caatinga (dry thorn-scrub) of the interior of Bahia. Because the flora of the caatingas of northeastern Brazil is still not well represented in herbaria (Mori, 1989), it is not possible to say just how rare *Cyrtocarpa caatingae* is. In addition, the herbarium labels on the older collections that represent this species provide almost no details about its habitat, habit, or phenology.

Cyrtocarpa caatingae resembles *C. procera* because of its paniculate inflorescence, lanceolate to narrowly elliptic leaflets, and glandular-mucronulate anther connective. The new species differs by its unilocular (vs. 2–5-locular) ovary, shorter stamens, and pistillode greatly exceeding (not exceeded by) the disk. While the occurrence of *Cyrtocarpa* in the semiarid climate of the caatingas is consistent with its habitat preference elsewhere, the ranges of the four species of *Cyrtocarpa* are markedly discontinuous (see Fig. 1), interrupted over long distances by moister habitats, or by water in the case of the two Mexican species.

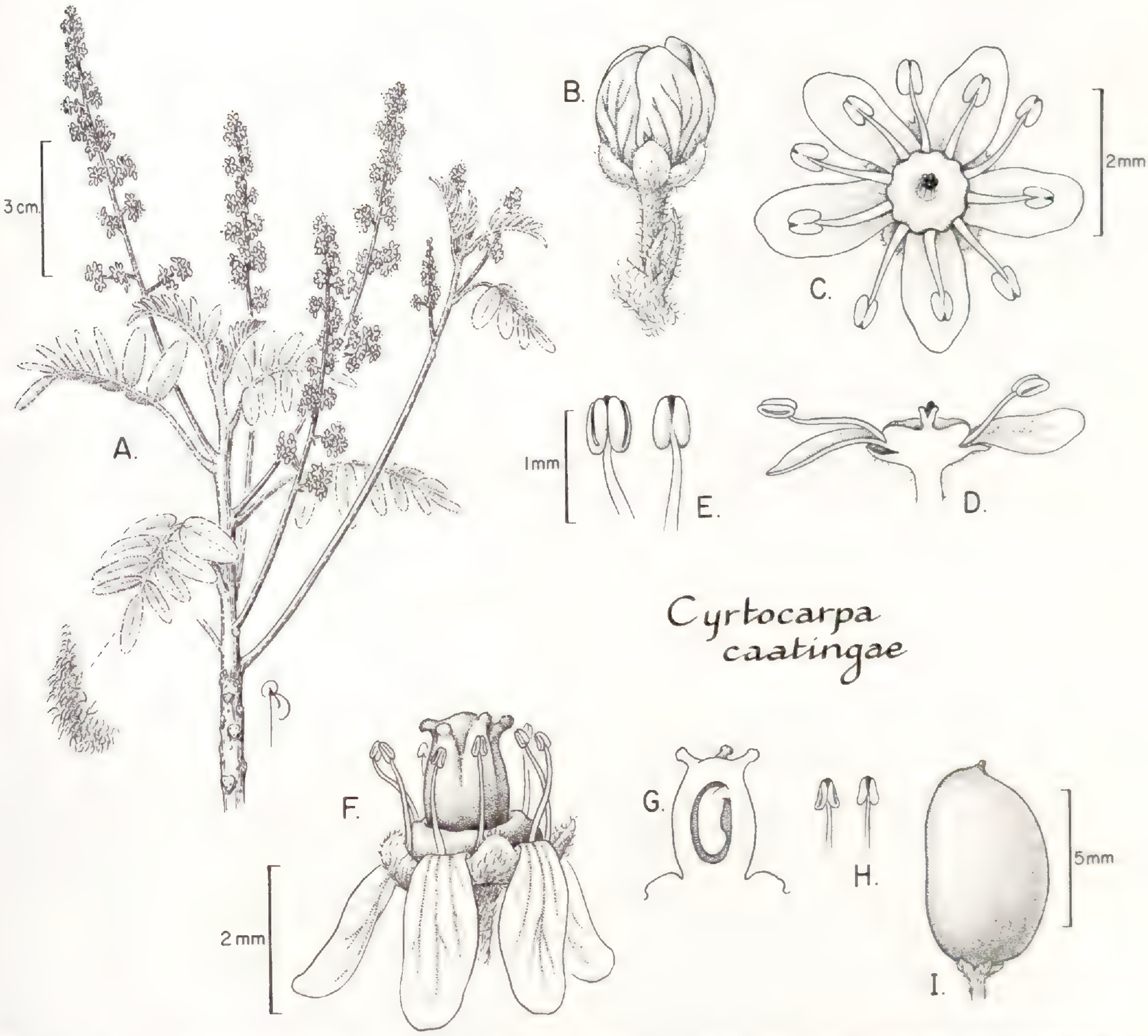

FIGURE 3. *Cyrtocarpa caatingae* Mitchell & Daly.—A. Staminate-flowering branchlet with immature leaves.—B. Opening flower.—C. Staminate flower at anthesis.—D. Longisection of flower, showing pistillode exceeding the disk.—E. Stamens, showing glandular-mucronulate anther connective.—F. Pistillate flower, post-anthesis.—G. Longisection of ovary, showing single locule.—H. Staminodes.—I. Immature fruit. Based on *Mori et al. 11248* (type; A–E), and *St. Hilaire s.n.* (F–I).

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STUDIES IN NEOTROPICAL PALEOBOTANY. VIII. THE PLIOCENE COMMUNITIES OF PANAMA—INTRODUCTION AND FERNS, GYMNOSPERMS, ANGIOSPERMS (MONOCOTS)[1]

Alan Graham[2]

ABSTRACT

Thirty-one fossil spores and pollen of ferns, gymnosperms, and monocotyledonous angiosperms have been identified from the Pliocene Gatun Formation of Panama together with one unidentified Pyrrophyta. These are *Lycopodium* (types 1–4), *Selaginella*, *Alsophila*, *Cnemidaria*, *Cyathea* (types 1, 2), *Ophioglossum*, *Grammitis*, *Ceratopteris*, *Pteris* (types 1–5), other trilete fern spores (types 1, 2), *Ctenitis* (types 1–3), other monolete fern spores (types 1–5), *Podocarpus*, Gramineae, and Palmae (types 1, 2). Pollen of dicotyledonous angiosperms (51 types, including 13 with no previously known fossil records) and 27 unknowns presently under study make the Gatun assemblage one of the largest Tertiary floras in northern Latin America. The remaining descriptions and interpretation of the flora will be presented in concluding papers.

In 1962 the Panama Canal Commission drilled a series of wells in Gatun Lake as part of the Trinidad Dam Project to test the foundation for increasing the water storage capacity of the lake. Samples from along these cores were obtained by Elso Barghoorn in 1962 and by the author in 1963. The upper portions of the cores were used by Bartlett & Barghoorn (1973) for study of Quaternary sea level and climatic changes in central Panama during the past 12,000 years. The lower portions penetrated subsurface Gatun Formation sediments, and these samples serve as the basis for the present study. It is fortunate that samples were preserved because subsequently all cores drilled by the Commission, representing millions of years of vegetational and paleoenvironmental history, were discarded because of storage limitations. All known surface exposures of the Gatun Formation are marine sediments (Fig. 1), and the core material is presently the only source of data on the vegetation of Panama during Gatun time. Core SL-49 was drilled at latitude 9°80′N + 4,113, longitude 79°57′W + 1,987, and levels 222.5, 223, and 233.5 (in feet, following original log data) yielded plant microfossils. Core SL-103 was drilled at latitude 9°16′N + 5,945, longitude 79°52′W + 2,963, and levels 250, 253, 255.5, and 257 yielded plant microfossils. Numbers following latitude and longitude (e.g., + 4,113) are the number of feet between the minute cited (e.g., 80′) and the next minute. They are used to locate precisely a site within a small or restricted locale.

The Gatun Formation was earlier assigned to the middle Miocene (Cooke et al., 1943; Stewart & Stewart, 1980; Woodring, 1957–1982), but marine invertebrate faunas now indicate a Pliocene age (Vokes, 1983; van den Bold, Stewart, pers. comm.). Other details on the location and geology of the Gatun and other Tertiary formations in Panama are summarized in Graham et al. (1985).

The Gatun Formation is the last and youngest in a series of five Tertiary pollen- and spore-bearing strata being studied from the Canal region of Panama. The others are the middle(?) to upper Eocene Gatuncillo Formation (Graham, 1985), and the lower Miocene Culebra, Cucaracha, and La Boca formations (Graham, 1988a, b, 1989). In addition, lower Miocene palynomorphs are known from the Uscari sequence of Costa Rica (Graham, 1987). Quaternary studies include those of Bartlett & Barghoorn (1973) on sediments from Gatun Lake, and Horn (1985) on sediments from DSDP site

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FIGURE 1. Surface outcrop of the Gatun Formation at Refinería Panama, near Colón, Panama. The dominant fossil is the marine gastropod *Turritella*. Several outcrops occur in the area, and all are marine sediments, lacking terrestrial plant microfossils. Terrestrial Gatun deposits are subsurface, and cores drilled by the Panama Canal Commission between 1950 and the 1960s have been discarded. Diameter of coin, 30 mm.

565 off western Costa Rica. In 1989, members of van der Hammen's group (pers. comm.) completed transects through the modern vegetation of Costa Rica preliminary to pollen and spore analysis of high-altitude peat deposits. Collectively, these studies will provide a more complete data base on Cenozoic vegetation and paleoenvironments for Panama and adjacent Costa Rica than for any other region of northern Latin America.

MATERIALS AND METHODS

Extraction and processing techniques are described in Graham (1985). Slides are labeled according to core number, depth, and slide number (e.g., SL-103, 253′, 1). Location of the specimens on the slides is by England Slide Finder coordinates (e.g., ESF G-40). All materials are deposited in the palynology collections at Kent State University.

SYSTEMATICS

Thirty-one palynomorphs are described from the Gatun Formation. One unidentified Pyrrophyta (dinoflagellate) was also recovered. Several are common in other fossil floras, and for these the information is synoptic. Present ranges and ecological data are based primarily on Tryon & Tryon (1982) for ferns, and on Croat (1978) and D'Arcy (1987) for gymnosperms and monocots. General stratigraphic ranges for the Caribbean region follow Germeraad et al. (1968) and Lorente (1986), with records from our previous studies listed separately. Other details on the systematics of the microfossils are discussed in Graham (1989: 51).

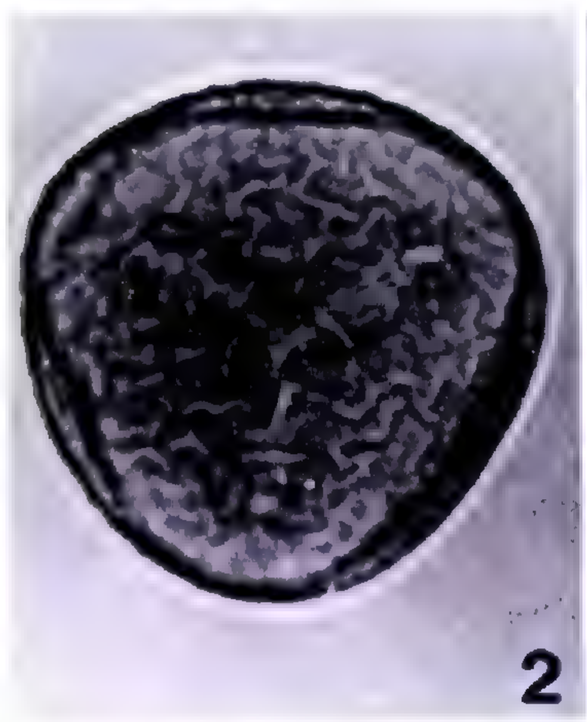
LYCOPODIACEAE

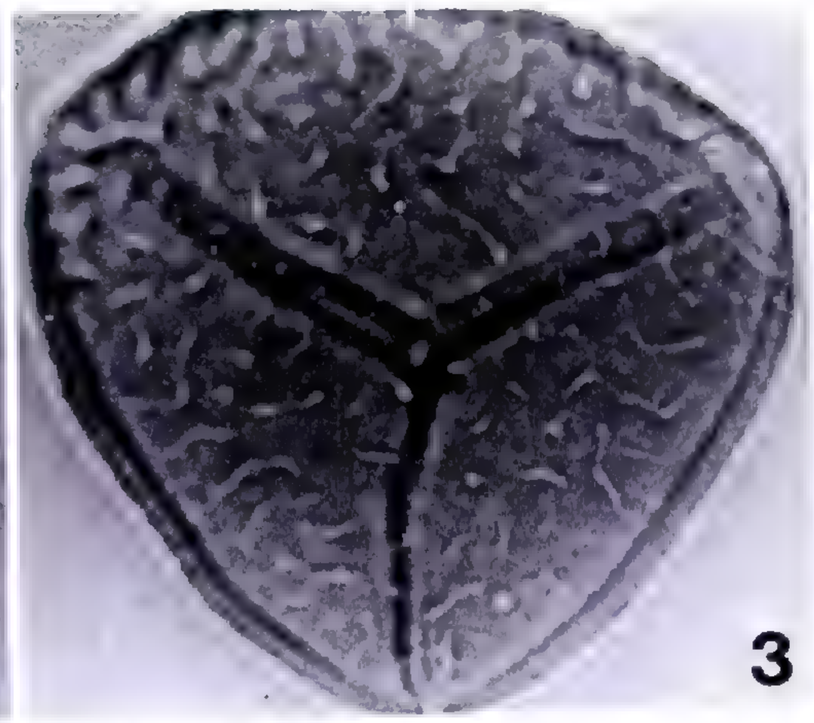
Lycopodium (type 1, Fig. 2). Amb oval-triangular to nearly circular, apices rounded; trilete, laesurae straight, narrow, ca. 12 μm long, extending ⅔ distance to spore margin, inner margin entire; distal surface reticulate, muri low, narrow (ca. 0.5 μm wide), smooth, sinuous, lumina irregular, occasionally appearing as narrow, sinuous, slitlike openings as viewed through the spore from the proximal surface, proximal surface laevigate; wall 2 μm thick, slightly thinner at apices; 36–39 μm.

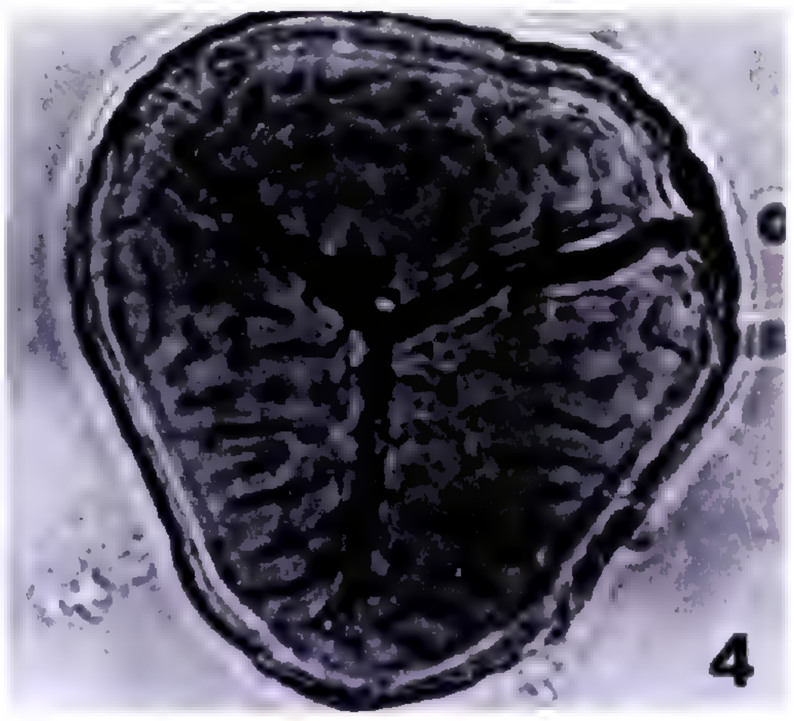
The reticulate spores of *Lycopodium* are characteristic of subg. *Lycopodium* (Wilce, 1972; Tryon & Tryon, 1982: 807), but the Gatun specimens cannot be referred to any individual species.

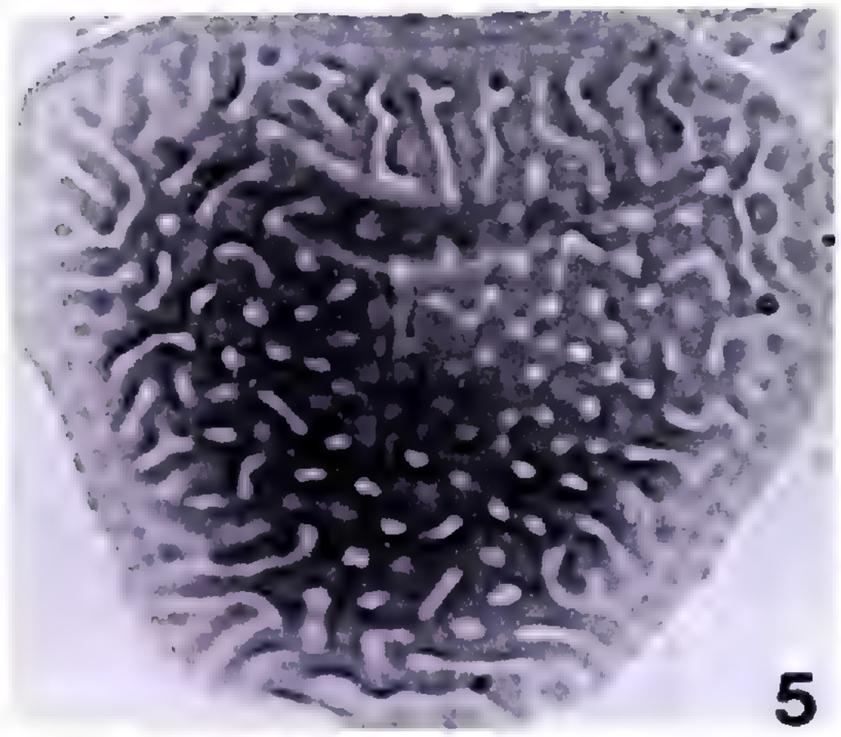
Lycopodium (type 2, Fig. 3). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, ca. 33 μm long, extending to spore margin, inner margin entire; distal surface with narrow, sinuous slitlike openings, proximal surface laevigate; wall 3 μm thick; 54–58 μm.

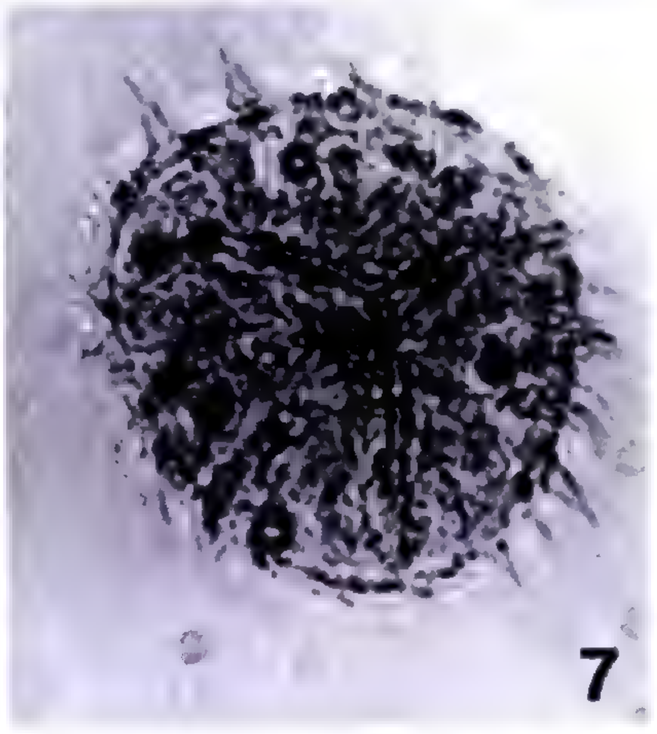
Lycopodium (type 3, Figs. 4, 5). Amb triangular to slightly concavo-triangular, apices rounded; laesurae straight, narrow, 22–24 μm long,











FIGURES 2–13. Fossil spores from the Gatun Formation.—2. *Lycopodium* type 1, SL-103, 253′ 4, ESF G-40.—3. *Lycopodium* type 2, SL-103, 253′, 5, ESF L-22.—4, 5. *Lycopodium* type 3, SL-103, 253′, 7, ESF K-21; SL-103, 253′, 10, ESF P-26.—6. *Lycopodium* type 4, SL-103, 253′, 4, ESF R-26.—7. *Selaginella*, SL-103, 253′,

extending ¾ to nearly to spore margin; distal surface with low verrucae/rugulae to nearly flat surface with spaces in between appearing as circular to narrow, elongated, slitlike openings, proximal surface laevigate; wall 2–3 μm thick; 50–60 μm.

These spores are similar to those of subg. *Cernuistachys* (Wilce, 1972; Tryon & Tryon, 1982: 807), including such species as *L.* (*Huperzia* fide Ollgaard, 1987) *hippuredeum* Christ.

Lycopodium (type 4, Fig. 6). Amb oval-triangular to nearly circular, apices rounded; trilete, laesurae straight, narrow, ca. 18 μm long, extending ¾ to nearly to spore margin, inner margin entire; distal surface foveolate, pits circular, 0.5 μm to slightly less in diameter, moderately dense, evenly spaced, proximal surface laevigate; wall 2 μm thick; 45–50 μm.

These spores are similar to those of subg. *Selago* (Wilce, 1972; Tryon & Tryon, 1982: 807), including *L. linifolium* L.

There are about 125 species of *Lycopodium* in the Neotropics growing as terrestrial or pendant epiphytes in a variety of habitats, including wet to damp sites in savannas, rainforests, cloud forests, and paramo.

The stratigraphic range for the various types of *Lycopodium* spores has not been summarized. Spores of *Lycopodium* have been reported previously in our studies from the San Sebastian, Uscari, Culebra, La Boca, and Paraje Solo formations.

SELAGINELLACEAE

Selaginella (Fig. 7). Amb oval-triangular to nearly circular, apices rounded; trilete, laesurae straight, narrow, ca. 12–15 μm long, extending ¾ to completely to spore margin, inner margin entire; distal surface echinate, spines ca. 3–6 μm long, base broad, occasionally giving reticulate appearance to spore surface, proximal surface laevigate to sparsely and minutely echinate; wall 2 μm thick; 30–38 μm (excluding spines).

There are about 250 species of tropical American *Selaginella*, growing primarily in mesic, damp, shaded forests and oak–pine woods, usually at elevations between sea level and 1,500 m, but with some species extending to 4,000 m (Tryon & Tryon, 1982: 820).

Spores of the *Selaginella* type are known in the stratigraphic literature as *Echitriletes* and range from Paleozoic to Recent. They are present in low percentages in the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, La Boca, and Paraje Solo formations.

CYATHEACEAE

Alsophila (Figs. 8–11). Amb triangular, apices rounded; laesurae straight, narrow, ca. 18 μm long (in smaller specimens, to ca. 28 μm in larger ones), inner margin entire, bordered by lip 4–6 μm wide, outer margin of lip frequently bordered by small (0.5 μm or less), circular pits; laevigate; wall 2 μm thick; 45–65 μm.

This description is based on the type illustrated in Figure 8, which is the most common one recovered from the Gatun sediments. Variations include larger size (Fig. 9), lip faint (Fig. 11) to nearly absent (Fig. 9), pits bordering laesurae faint to conspicuous, laesurae closed (Fig. 9) or open (Fig. 10), and occasional branching of the laesurae apices (Fig. 11).

The designation of fossil spores as *Alsophila* vs. *Cyathea* is almost arbitrary because of the differing classifications of tree ferns (e.g., Holttum 1964, 1965; Tryon, 1970; Tryon & Tryon, 1982: 182) and the consequent labeling of herbarium specimens from which spore reference material is obtained. Laevigate or nearly laevigate fossil spores are provisionally referred to *Alsophila*, while micropunctate ones (Fig. 14) are referred to *Cyathea* (Graham, 1989: 55).

Alsophila is a genus of about 13 tropical American species. It usually grows in cloud forests, wet montane or elfin forests, primarily as an understory species, at elevations from about 1,000 to 2,000 m.

Spores of *Alsophila*, as defined here, are known from the San Sebastian and Paraje Solo formations (as *Cyathea* in both).

Cnemidaria (Figs. 12, 13). Amb oval-triangular, apices rounded; trilete, laesurae straight, narrow, 20–25 μm long, extending ca. ¾ to nearly to spore margin, inner margin entire, bordered by occasional faint lip 3–5 μm wide; foveolate, smaller pits (1–6 μm diam.) numerous, irregularly scattered over spore surface, larger pits (12–15 μm)

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9, ESF S-41.—8–11. *Alsophila*, SL-103, 253′, 11, ESF 0-22; SL-103, 253′, 4, ESF N-17; SL-103, 253′, 2, ESF J-42; SL-103, 253′, 16, ESF E-32.—12, 13. *Cnemidaria*, SL-103, 253′, 15, ESF Y-24; SL-103, 257′, G-12. All photographs taken at 400×; size in microns given in descriptions.

typically 3, symmetrically arranged one each between arms of trilete scar along spore periphery; wall 2–3 μm thick; 40–50 μm.

Cnemidaria is a tropical American tree fern genus of 25 species (Tryon & Tryon, 1982: 209), typically growing in deep-shaded, wet, montane forests, and along stream banks and waterfalls, at elevations up to about 1,500 m.

Spores of *Cnemidaria* have been reported from the San Sebastian (under the name *Hemitelia*), Uscari, and Paraje Solo (as *Hemitelia*) formations.

Cyathea (type 1, Fig. 14). Amb triangular, apices rounded; trilete, laesurae straight, narrow, 30 μm long, extending ¾ distance to spore margin, inner margin entire, bordered by faint lip 3–4 μm wide; distal surface micropunctate, proximal surface laevigate; wall 2 μm thick; 58–65 μm.

These fossil spores are similar to spores of *C. petiola* (Hook.) Tryon and *C. speciosa* Willd. (Tryon & Tryon, 1982: 207, fig. 20).

Cyathea (type 2, Figs. 15–17). Amb oval-triangular, margin lobate due to projecting sculpture elements, apices rounded; trilete, laesurae straight, narrow, 18–20 μm long, extending ¾ to nearly to spore margin, inner margin entire; distal surface with conspicuous, moundlike verrucae, 6–7 μm diam., smooth, proximal surface laevigate; wall 3 μm thick; 45–62 μm.

These spores are similar to those of several species of *Cyathea*, including *C. caracasana* (Kl.) Domin (Tryon & Tryon, 1982: 207, fig. 17).

As defined by Tryon & Tryon (1982: 204) *Cyathea* is a tropical American genus of 40 species, growing primarily in montane and cloud forests, more rarely in lowland rainforests, and typically at elevations between 1,500 and 2,000 m.

Spores of *Cyathea* are known from the Culebra, Cucaracha, La Boca, and Paraje Solo formations.

OPHIOGLOSSACEAE

Ophioglossum (Fig. 18). Amb oval-triangular to nearly circular, apices rounded, margin lobate due to projecting sculpture elements; trilete, laesurae straight, narrow, 32–34 μm long, extending to spore margin, inner margin entire; verrucate, apices of verrucae rounded to broadly pointed, spore surface between verrucae with irregular to elongated, slitlike punctae; wall 3–4 μm thick; 70–76 μm.

About 10 species of *Ophioglossum* occur in the American tropics. They grow in a wide variety of habitats, often in open woods, savannas, and marshy areas, and usually at elevations between 500 and 3,000 m (Tryon & Tryon, 1982: 36).

Stratigraphic palynologists place *Ophioglossum* spores in the artificial genus *Foveotriletes*, and in the Caribbean region these range from the Upper Cretaceous (Maastrichtian) to Recent. They have not been reported previously from our Gulf/Caribbean Tertiary assemblages.

POLYPODIACEAE

Grammitis (Fig. 19). Amb oval-triangular, apices rounded, margin faintly lobate due to projecting sculpture elements; trilete, laesurae straight, narrow, 17–19 μm long, extending to or nearly to spore margin, inner margin entire; verrucate, verrucae small (ca. 2 × 1.5–2 μm), apex often truncate, densely arranged; wall 2 μm thick; 42–46 μm.

There are about 175 American species of *Grammitis*, growing primarily in wet habitats in cloud and elfin forests at elevations typically between 2,000 and 3,000 m. The fossil spores are similar to those of several living species, including *G. kalbreyeri* (Baker) Morton, common in Central America.

Spores of *Grammitis* have not been reported previously from our Gulf/Caribbean assemblages.

PTERIDACEAE

Ceratopteris (Fig. 20). Amb oval-triangular to circular, apices rounded; trilete, laesurae straight, narrow, 30–32 μm, extending ½ to ⅔ distance to spore margin; striate, striae in numerous, broad, flat, smooth bands 4–5 μm wide, area between bands 1–2 μm wide; wall 2–3 μm thick; 68–72 μm.

In tropical America *Ceratopteris* consists of two closely related species of floating ferns [*C. pteri-*

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FIGURES 14–25. Fossil spores from the Gatun Formation.—14. *Cyathea* type 1, SL-103, 255.5′, 5, ESF V-32.—15–17. *Cyathea* type 2, SL-103, 253′, 9, ESF H-22, D-41; SL-103, 253′, 11, ESF N-48.—18. *Ophioglossum*, SL-103, 253′, 6, ESF X-49.—19. *Grammitis*, SL-103, 253′, 6, ESF Q-38.—20. *Ceratopteris*, SL-48, 162′, 1, Q-30.—21. *Pteris* type 1, SL-103, 253′, 1, ESF U-41.—22. *Pteris* type 2, SL-103, 253′, 7, ESF K-24.—23. *Pteris* type 3, SL-49, 222.5′, 1, ESF J-18.—24. *Pteris* type 4, SL-103, 253′, 1, ESF H-47.—25. *Pteris* type 5, SL-103, 253′, 12, ESF M-42.

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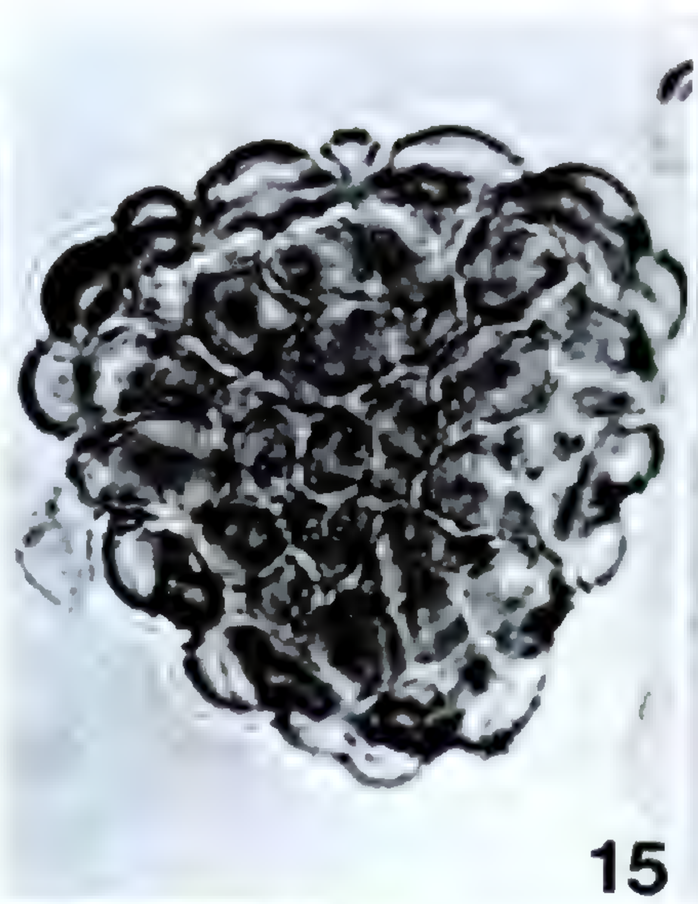

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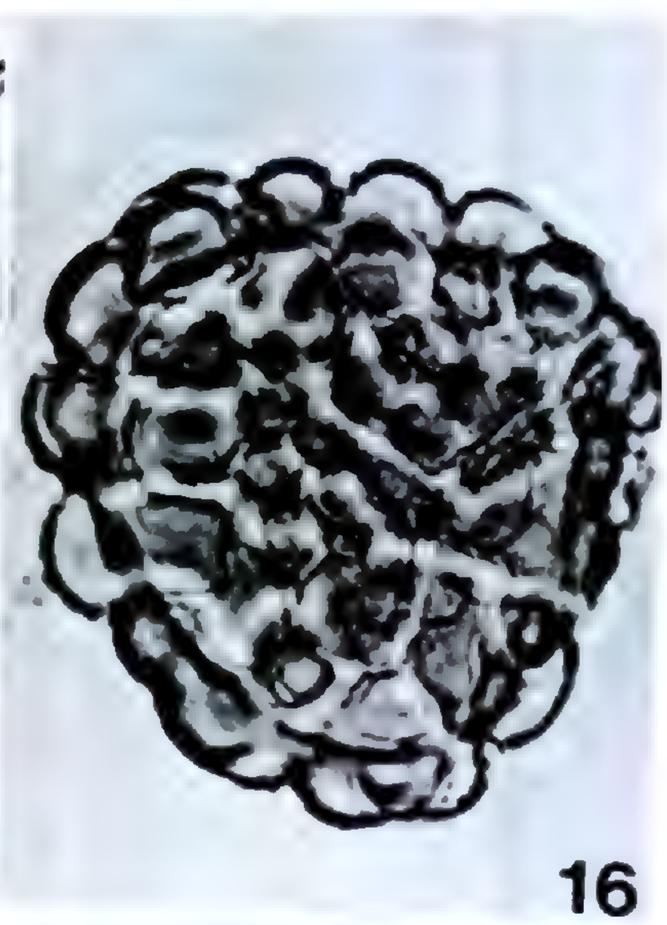

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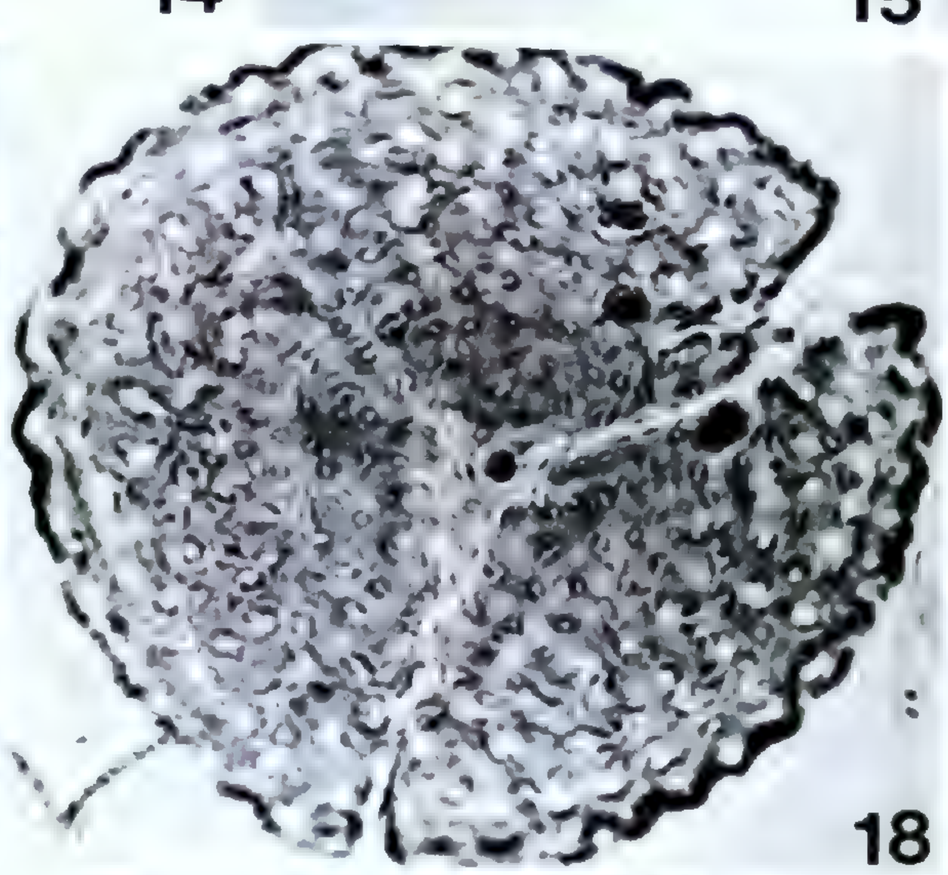

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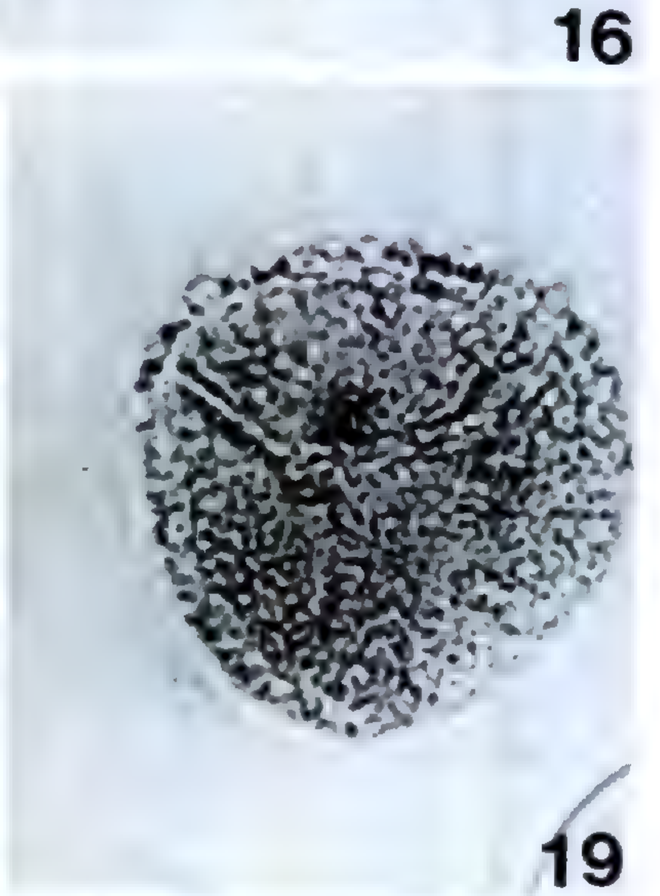

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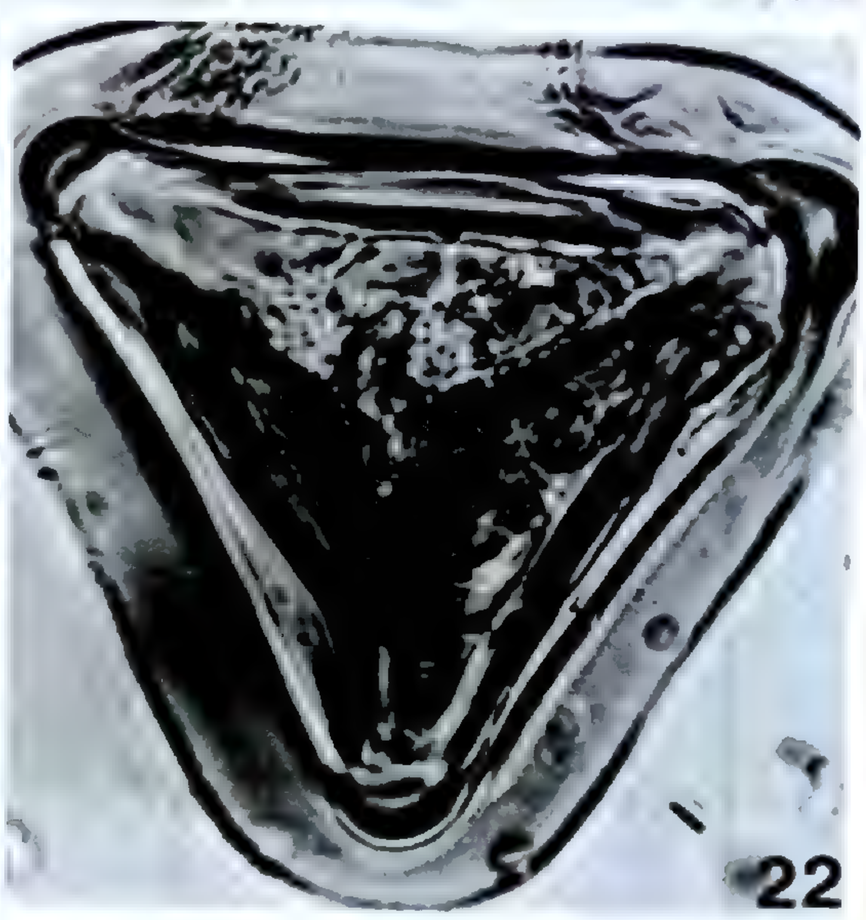

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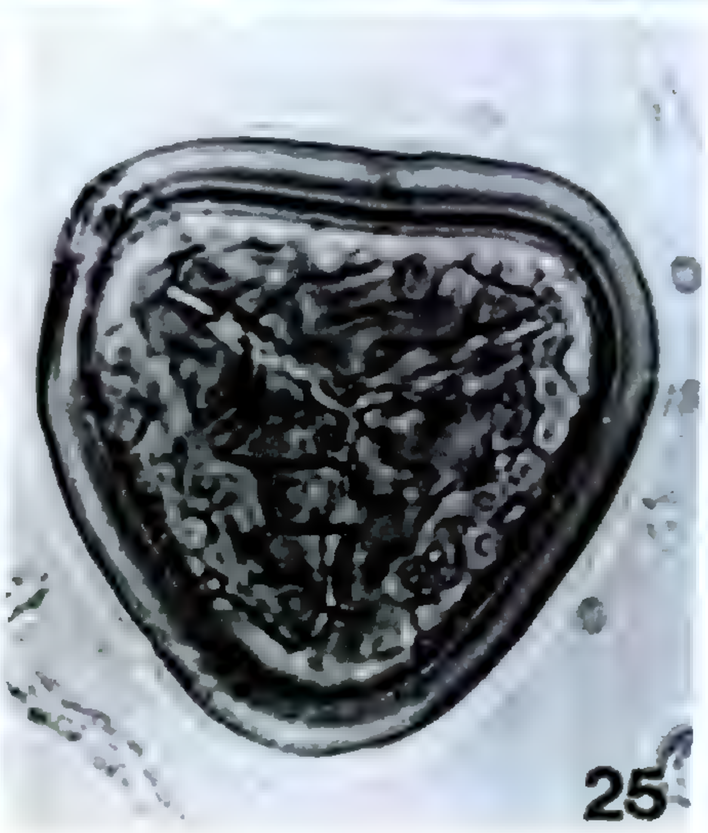

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doides (Hook.) Hieron. and *C. thalictroides* (L.) Brongn.] commonly found in fresh water but occasionally in brackish water habitats. They occur in ditches, lagoons, rivers, lakes, or rooted in wet soil or shallow water, usually between sea level and 300 m (Tryon & Tryon, 1982: 315). No consistent differences could be detected between the spores of the two modern species.

Fossil specimens are known in the stratigraphic literature as *Magnastriatites* and in the Caribbean area were previously listed as ranging from the base of the Oligocene to Recent, but the Gatuncillo report (Graham, 1985) extends the genus back to the middle(?) to upper Eocene. Other records are from the Cucaracha and Paraje Solo formations.

Pteris (type 1, Fig. 21). Amb oval, apices rounded; laesurae straight, narrow, 20–24 μm long, extending to spore margin, inner margin entire; conspicuous flange present, 8–10 μm wide, smooth, outer flange margin entire; distal surface laevigate, proximal surface with few low, flat, shieldlike verrucae; wall 2 μm thick; 52–65 μm.

Pteris type-2 spores (Fig. 22) are larger (80–86 μm), and have a few, large verrucae scattered over the distal surface. Type 3 (59–64 μm, Fig. 23) have numerous, low, flat verrucae with sinuous slitlike spaces between the verrucae. Type 4 (47–66 μm, Fig. 24) have low, smooth, elongated, sinuous verrucae/rugulae. Type 5 (47–51 μm, Fig. 25) have numerous, blocky, angular verrucae. There is a considerable range in variation among modern spores, both within and between species, and these fossil morphotypes cannot be referred consistently to any single species.

About 55 species of *Pteris* occur in the American tropics in a wide variety of habitats. Most are found "in wet forests, at the edge of clearings, in thickets, sometimes in cloud forests or in gallery forests, or occasionally on cliffs," generally at lower altitudes between sea level and about 2,000 m (Tryon & Tryon, 1982: 338).

The spores are known in the stratigraphic literature as *Polypodiaceoisporites* (Lorente, 1986: 154) and are known from the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, La Boca, and Paraje Solo formations.

OTHER TRILETE FERN SPORES

Several trilete fern spores were recovered that could not be identified. Two of the most common and/or distinctive ones are described below.

Type 1 (Figs. 26, 27). Amb triangular, apices rounded; trilete, laesurae straight, narrow, 20–24 μm, extending to or nearly to spore margin, bordered by faint lip 6–8 μm wide, inner margin entire; spore surface with irregular, slightly raised segments 9–12 μm diam., each with numerous, minute baculae/clavae; wall 3 μm thick; 38–52 μm.

These specimens were originally interpreted as slightly corroded *Cyathea* spores, but ultimately many were recovered with the same characteristic ornamentation. The spore has not been recorded previously in our Gulf/Caribbean Tertiary assemblages.

Type 2 (Fig. 28). Amb circular; trilete, laesurae straight, narrow, 16–18 μm long, extending ¾ to nearly to spore margin, inner margin entire; echinate, echinae small (ca. 0.5 μm), numerous and densely distributed; wall 1–2 μm thick; 43–47 μm.

DRYOPTERIDACEAE

Ctenitis (type 1, Fig. 29). Reniform; monolete, laesurae straight, narrow, 19–23 μm long, inner margin entire; echinate, echinae numerous, delicate, narrow, ca. 2 μm long, curved, frequently appearing appressed to spore surface; wall 3 μm thick; 38–40 × 24–29 μm.

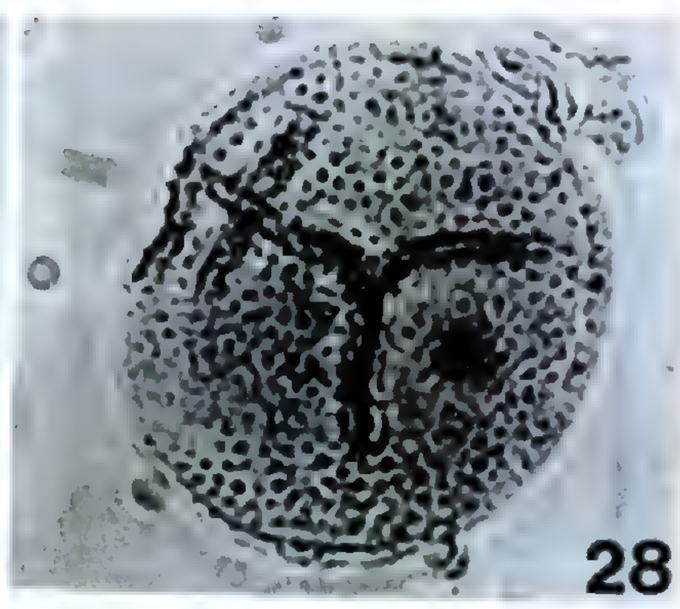
In type 2 (30–38 × 28–32 μm, Fig. 30) the spines are more straight and do not appear appressed to the spore surface. In type 3 (40–45 × 34–36 μm, Fig. 31) the spines are longer (ca. 3–4 μm) and somewhat fewer in number. Spores of several modern species also exhibit these variations [*Ctenitis* (= *Megalastrum*) *acrosorum* (Hieron.) Smith & Morgan (1987)], and the fossils cannot be referred to any one species. About 75 species of *Ctenitis* occur in the American tropics, primarily in wet forests, and most frequently at elevations between about 500 and 1,800 m (Tryon & Tryon, 1982: 463). Spores of *Ctenitis* have not been reported previously in our Gulf/Caribbean assemblages.

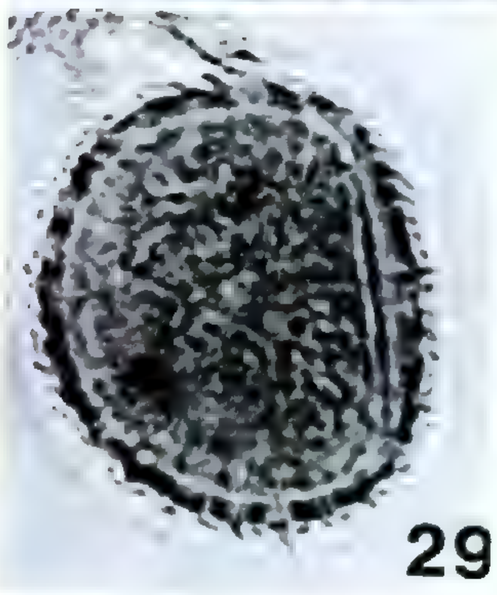
OTHER MONOLETE FERN SPORES

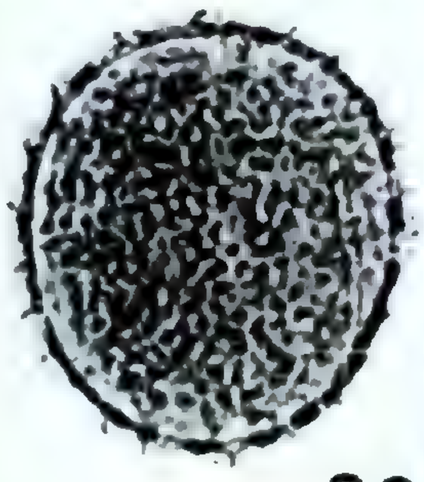
In addition to *Ctenitis*, several other monolete fern spores were recovered that could not be identified. Several of the most common and/or distinctive ones are described below.

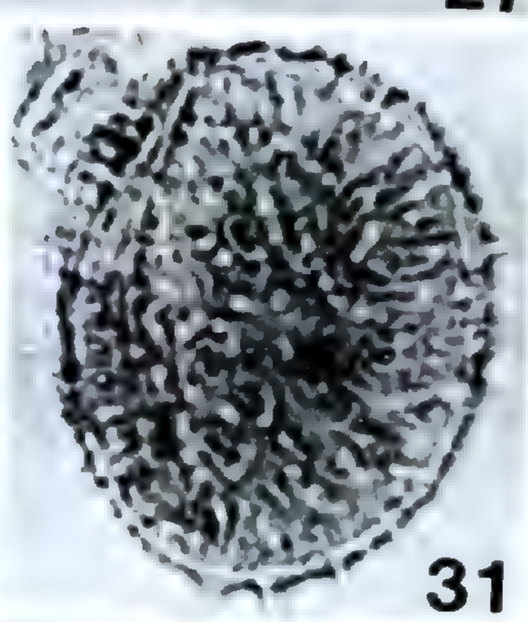
Type 1 (Fig. 32). Reniform; monolete, laesurae straight, narrow, 16–20 μm long, inner margin entire; laevigate; wall 2 μm thick; 55–48 × 33–39 μm.

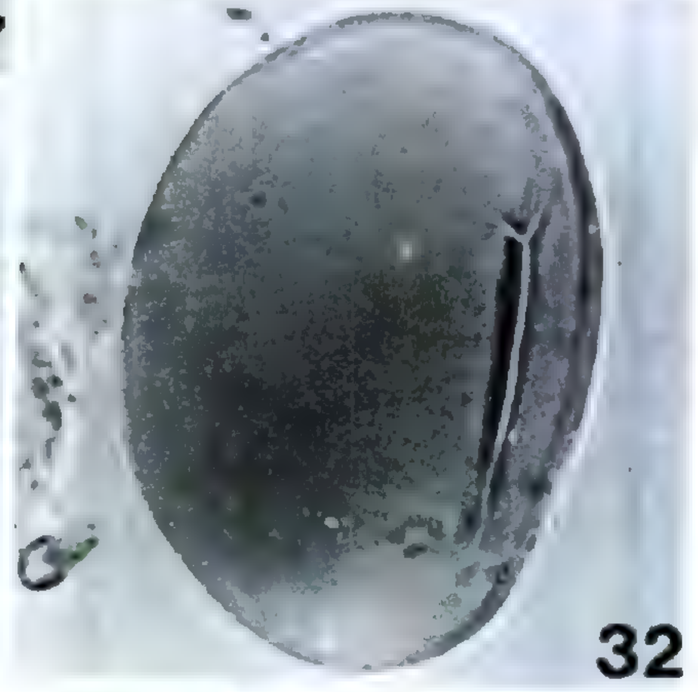
Monolete laevigate spores lacking the ornamented perine (*Laevigatisporites*) are common in fossil deposits, ranging from Paleozoic to Recent,

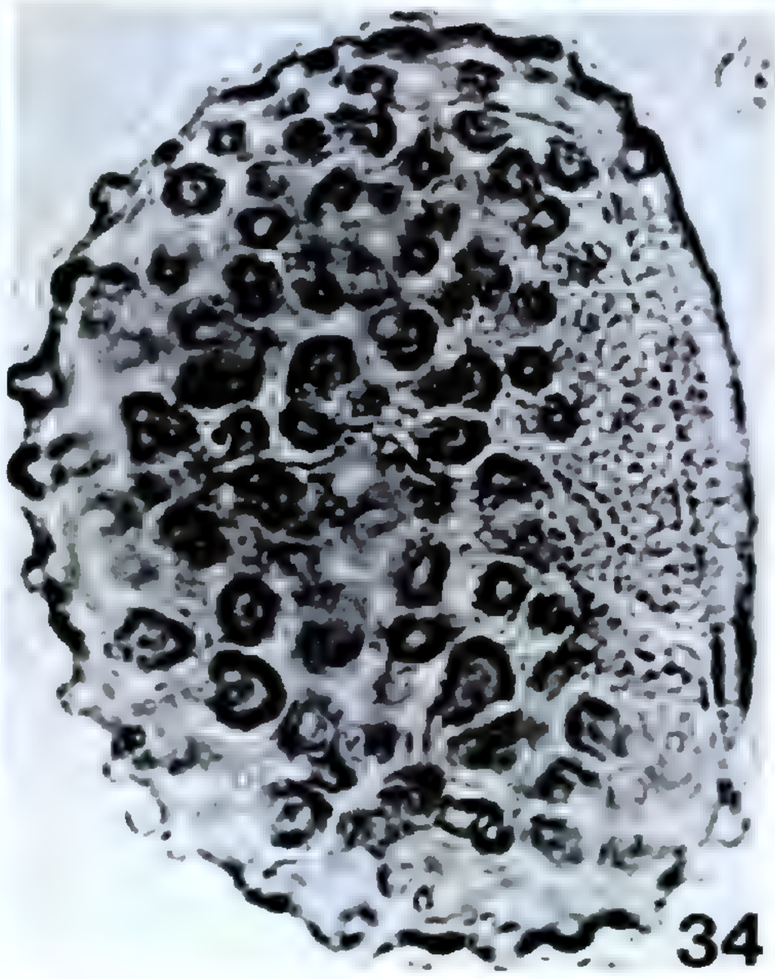


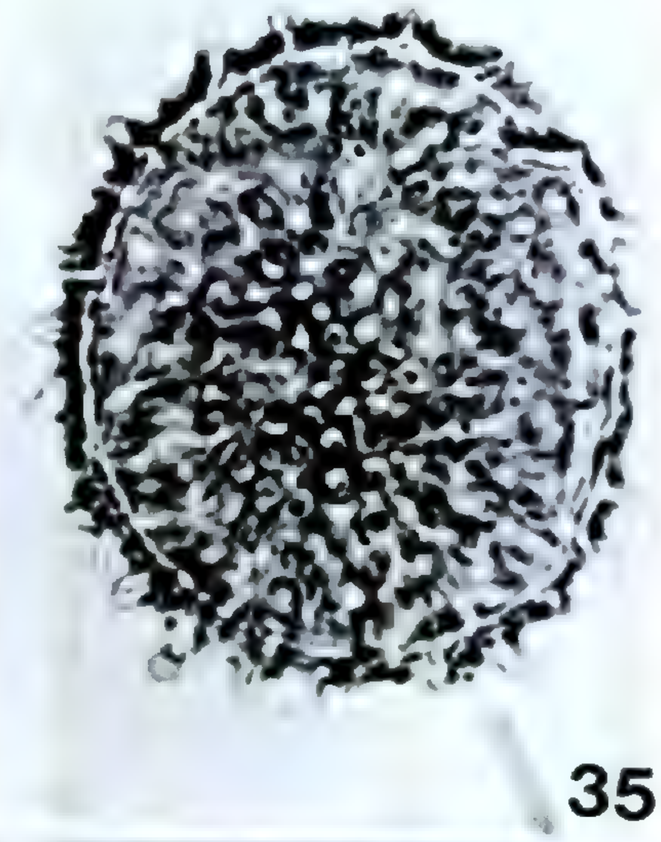


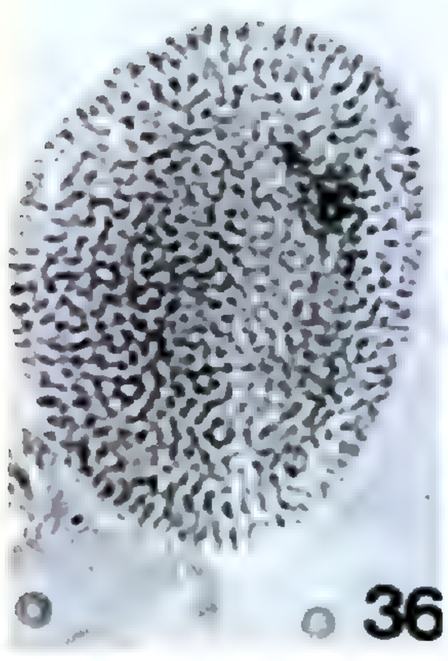


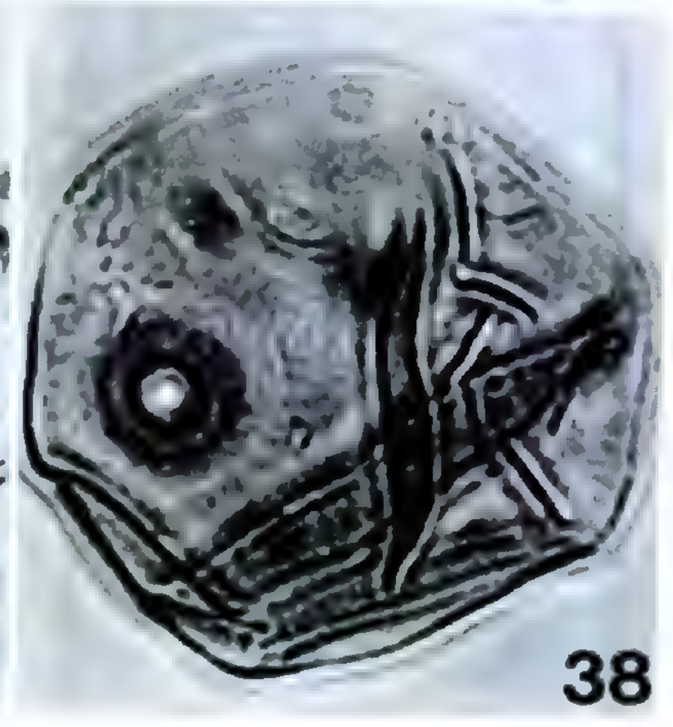












FIGURES 26–38. Fossil spores and pollen from the Gatun Formation.—26, 27. Trilete fern spore type 1, SL-103, 253′, 6, ESF 41; SL-103, 253′, 2, ESF H-48.—28. Trilete fern spore type 2, SL-103, 253′, 9, ESF U-28.—29. *Ctenitis* type 1, SL-103, 253′, 10, ESF N-52.—30. *Ctenitis* type 2, SL-103, 257′, 1, ESF N-15.—31. *Ctenitis* type 3, SL-103, 253′, 12, ESF M-32.—32. Monolete fern spore type 1, SL-103, 253′, 1, ESF O-30.—33. Monolete fern spore type 2, SL-103, 253′, 1, ESF G-46.—34. Monolete fern spore type 3, SL-103, 253′, 9, ESF Q-26.—35. Monolete fern spore type 4, SL-103, 253′, 15, ESF T-44.—36. Monolete fern spore type 5, SL-103, 253′, 1, ESF T-32.—37. *Podocarpus*, SL-103, 253′, 7, ESF J-30.—38. Gramineae, SL-103, 255.5′, 5, ESF Q-36.

and are produced by numerous Blechnaceae, Polypodiaceae, and Pteridaceae.

Type 2 (69–88 × 45–68 μm, Fig. 33) differs from type 1 in being moderately verrucate, while type 3 (85–88 × 55–58 μm, Fig. 34) has more conspicuous verrucae that taper to blunt apices. Both are placed in the artificial genus *Verrucatisporites*, range from Paleozoic to Recent, and are produced by numerous Blechnaceae, Polypodiaceae, and Pteridaceae. Type 4 (48–52 μm in length, Fig. 35) is similar to some *Ctenitis* spores, but type 4 spores are larger, and the spines (3 μm) are more coarse (broader) and the apices are blunt. Type 5 (42–48 × 30–36 μm, Fig. 36) has small (ca. 0.5 μm), fine, clavate to baculate/echinate sculpture elements. None of these can be referred to types presently in our reference collection.

Types 1–3 are common in all our Gulf/Caribbean assemblages, while types 4 and 5 have not been recovered previously.

PODOCARPACEAE

Podocarpus (Fig. 37). Bisaccate; monocolpate, colpus situated between air sacs, margin diffuse, 25–30 μm long, body amb circular, finely verrucate, some sculpture elements elongated forming rugulae, occasionally anastomosing, outer margin lobate, 40–44 μm, body wall 1 μm thick; air sacs two, hemispheric, 45–48 × 36–39 μm, large in relation to body size (compared to other vesiculate gymnosperm pollen), reticulate, muri low, narrow (ca. 1 μm), smooth, lumina irregular in shape and diameter (larger 5–6 μm); overall dimensions (including air sacs) 75–90 × 40–50 μm.

Three species of *Podocarpus* occur in Panama (D'Arcy, 1987): *P. guatemalensis* Standl. (also in Costa Rica and Guatemala), *P. magnifolius* Buch. & N. E. Gray (Guianas, Venezuela), and *P. oleifolius* D. Don. (Costa Rica, Colombia, Ecuador, Peru, Venezuela). The trees grow primarily in mid- to high-altitude cloud forests at elevations between about 1,000 and 2,000 m and are frequently associated with temperate elements such as *Alnus*, *Ilex*, *Myrica*, and *Quercus*. The fossil specimens are similar to *P. oleifolius*, but pollen of the other species are not represented in our reference collection, or by pollinating material at F, MO, and US.

Podocarpus has been reported previously from the San Sebastian, Uscari, and Paraje Solo formations. It is also known from the Oligo–Miocene Simojovel Group of Chiapas, Mexico (Langenheim et al., 1967).

GRAMINEAE (Fig. 38)

Spherical, amb circular; monoporate, pore circular, 3–4 μm diam., inner margin entire, surrounded by annulus 3–4 μm wide; psilate to scabrate; tectate, wall 1–2 μm thick; 36–44 μm.

The Gramineae are a stenopalynous family, and the fossil pollen cannot be referred to individual genera. In the stratigraphic literature they are known as *Monoporites*, and in the Caribbean region range from the Paleocene but become abundant beginning only in the lower Eocene. Grass pollen occurs in the Culebra, La Boca, and Paraje Solo formations. It has also been reported (as *Graminidites*) from the Eocene of Cuba (Areces-Mallea, 1988).

PALMAE

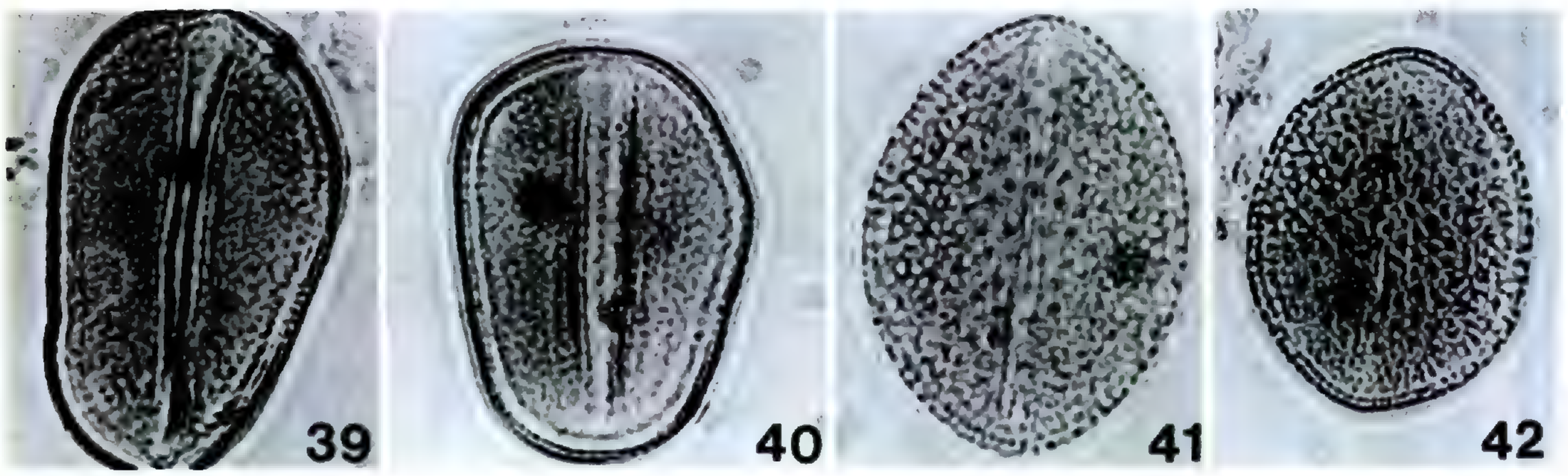
There is considerable diversity in pollen of modern palms (Ferguson, 1986; Thanikaimoni, 1970), but still many types are common to more than one genus and most fossils cannot be identified below the level of family. Two types were recovered from the Gatun sediments.

Type 1 (Figs. 39, 40). Amb cuneiform (wedge-shaped, broadest above equator); monocolpate, colpus straight, 40–44 μm long, extending nearly entire length of grain, sides parallel for most of colpus length, apices blunt to slightly rounded, inner margin minutely dentate; scabrate; tectate, wall 2 μm thick; 47–58 × 33–38 μm.

The pollen is similar to that of *Aiphanes*, *Manicaria*, *Reinhardtia*, and the monocolpate forms of predominately trichotomosulcate genera such as *Acrocomia*. Similar pollen has been reported previously from the Gatuncillo, Culebra, Cucaracha, La Boca, and Paraje Solo formations.

Type 2 (Figs. 41, 42). Amb oval; monocolpate, colpus straight, 33–35 μm long, extending nearly entire length of grains, sides parallel for most of colpus length, apices blunt to slightly rounded, inner margin entire to minutely dentate; reticulate, muri low, smooth, relatively thick (1.5 μm) compared to diameter of lumina (2 μm), underlying columellae evident giving reticulum faintly beaded appearance, occasional free sexine elements within lumina; tectate-perforate, wall 2 μm thick; 43–45 × 35–37 μm.

This pollen type is similar to that of *Colpothrinax*, *Cryosophila*, and *Neonicholsonia*. Pollen with these characteristics has not been reported previously in our Gulf/Caribbean assemblages.



FIGURES 39–42. Fossil pollen from the Gatun Formation.—39, 40. Palmae type 1, SL-103, 253′, 7, ESF P-23; SL-103, 253′, 6, S-44.—41, 42. Palmae type 2, SL-103, 253′, 9, ESF Q-23; SL-103, 253′, 5, ESF J-48.

In addition to the 31 spore and pollen types described here, 51 kinds of dicotyledonous pollen have been identified from the Gatun Formation, including 13 with no previously known fossil record. There are also 27 unknowns presently under study. This makes the Gatun assemblage, with 110 types, including one unidentified Pyrrophyta (dinoflagellate), the second largest Tertiary fossil flora known from northern Latin America (the largest is the middle Pliocene Paraje Solo flora from Veracruz, Mexico, with approximately 124 types; Graham, 1976). The remaining descriptions, and interpretation of the flora, will be presented in subsequent papers in the series.

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STUDIES IN NEOTROPICAL PALEOBOTANY. IX. THE PLIOCENE COMMUNITIES OF PANAMA—ANGIOSPERMS (DICOTS)[1]

Alan Graham[2]

Abstract

Fifty-one fossil dicotyledonous pollen types and 27 unknowns are described from the Pliocene Gatun Formation of Panama. These are *Cymbopetalum*, *Ilex*, cf. *Aguiaria*, *Bernoullia*, *Ceiba*, *Pseudobombax*, *Bursera*, cf. *Bucida*, *Combretum/Terminalia*, Mutisieae type, cf. *Cionosicys*, Ericaceae (types 1, 2), *Alchornea*, cf. *Glycydendrum*, cf. *Jatropha*, cf. *Stillingia*, *Quercus*, *Alfaroa/Oreomunnea*, *Acacia*, *Crudia*, *Erythrina*, *Utricularia*, Loranthaceae (types 1, 2), Malpighiaceae (types 1, 2), *Hampea/Hibiscus*, Melastomataceae, *Cedrela*, *Guarea*, *Eugenia/Myrcia*, *Cabomba*, *Hauya*, *Rhizophora*, *Chomelia* type, *Cosmibuena*, *Faramea* (types 1, 2), *Posoqueria*, *Casimiroa*, *Allophylus*, *Cupania*, *Paullinia*, *Serjania*, cf. *Bumelia*, *Symplocos* (types 1, 2), *Mortoniodendron*, *Aegiphila*, and *Petrea*. Spores of the lycopods and ferns, and pollen of the gymnosperms and monocotyledenous angiosperms, have been described previously. Paleoecological and paleoenvironmental interpretations will be presented in a concluding paper.

This paper completes the systematic treatment of plant microfossils recovered from the Pliocene Gatun Formation of Panama. Introductory material and the systematics of other groups (ferns, gymnosperms, and monocots) are given in Graham (1991), new records of previously unreported taxa are provided in Graham (1990), and the geology of the pollen-bearing deposits is summarized in Graham et al. (1985). Fifty-one dicotyledonous pollen types, together with 27 unknowns, are recognized here. Thirty-one fern, gymnosperm, and monocot microfossils, and one Pyrrophyta (dinoflagellate), were previously reported, bringing the total number of taxa to 110. Numerical representations, and paleocommunity and paleoenvironmental reconstructions will be presented in a concluding paper.

Materials and Methods

Extraction and processing techniques are described in Graham (1985). Slides are labeled according to core number, depth, and slide number (e.g., SL-103, 253′ [feet], 2). Location of the specimens on the slides is by England Slide Finder coordinates (e.g., ESF L-44). Details of interwall morphology (e.g., homogeneous; columellae just visible) are described as seen in median optical section with light microscopy at the magnification indicated (e.g., 400×). All materials are deposited in the palynology collections at Kent State University.

Systematics

ANNONACEAE

Cymbopetalum (Figs. 1, 2). Oblate, amb circular; nonaperturate(?); psilate; tectate-perforate, tectal perforations large, circular to irregular in outline, constituting ca. 40–50% of grain surface, columellae conspicuous, ca. 15 μm long; 180 μm.

Cymbopetalum consists of 11 to 13 species of trees and shrubs distributed from Mexico to tropical South America, with three species in Panama: *C. brasiliense* (Vell.) Benth., *C. costaricense* (J. D. Smith) R. E. Fries, and *C. languipetalum* Schery. Pollen of the modern species has been studied by Walker (1971a, b, c, 1972). *Cymbopetalum* is known only from the Gatun assemblage.

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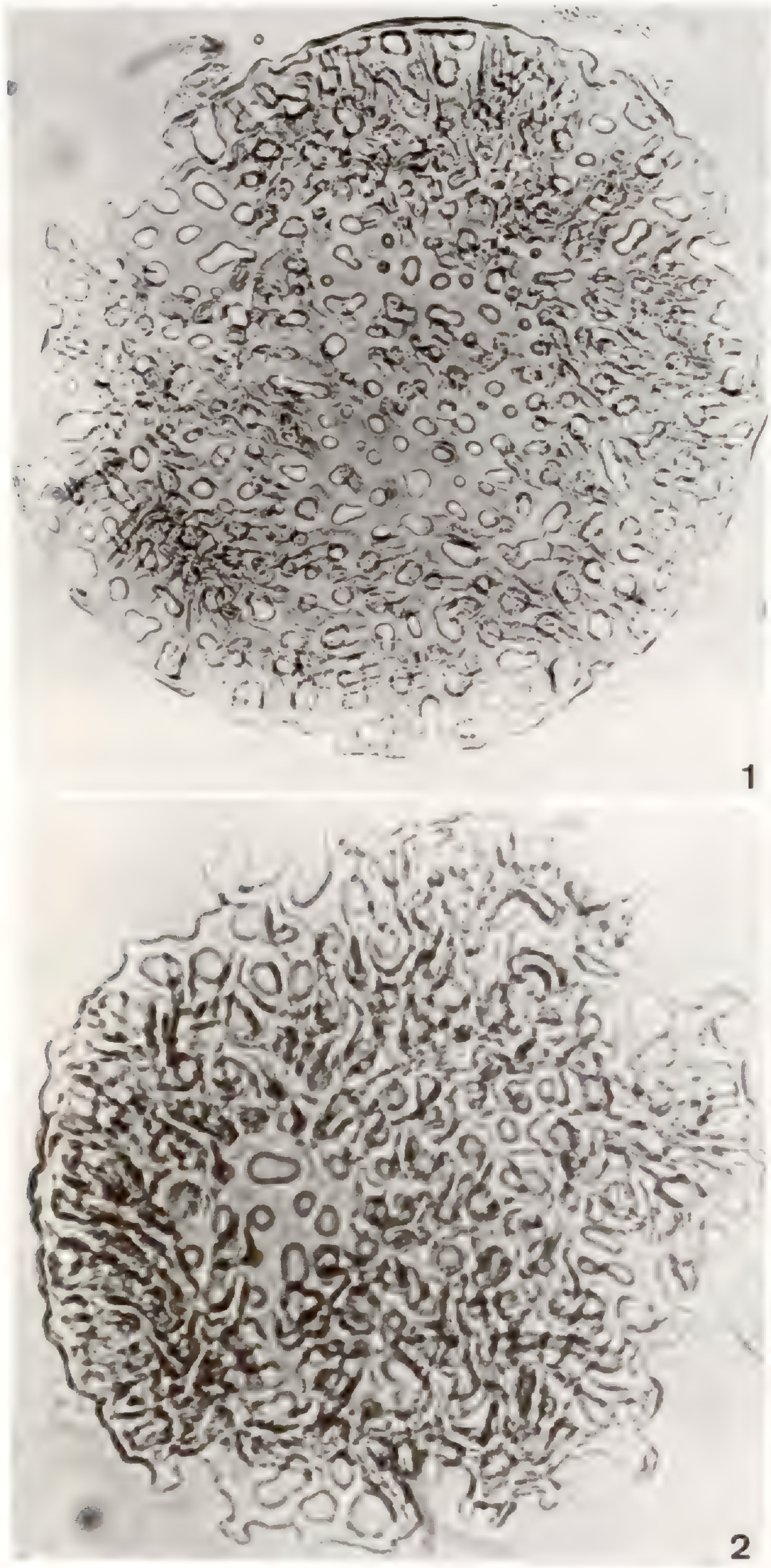
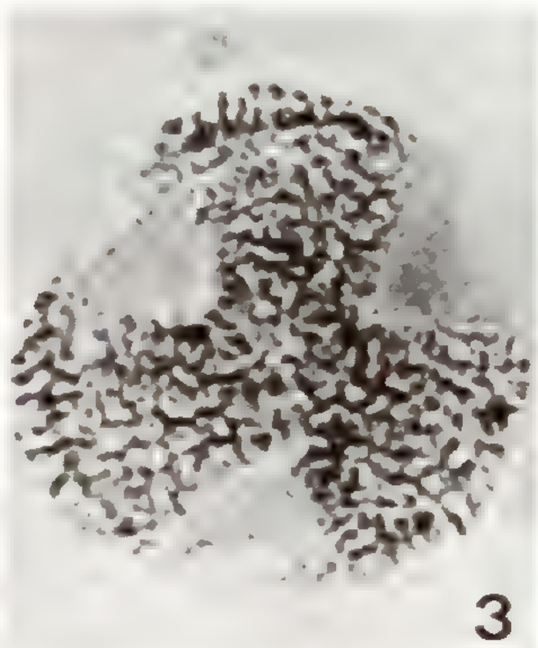
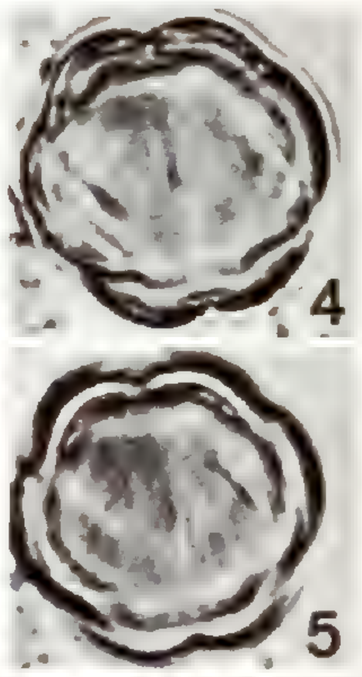
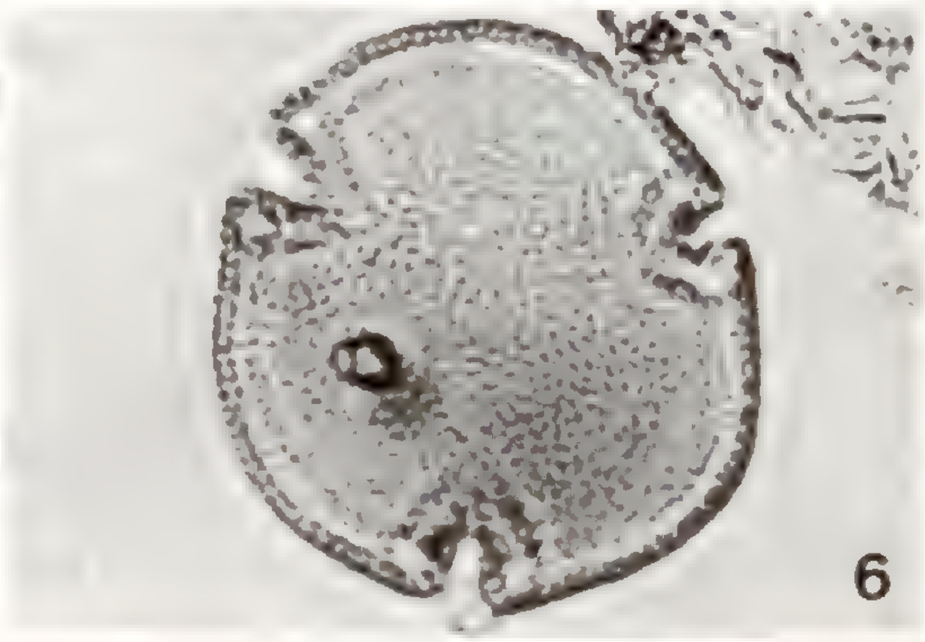
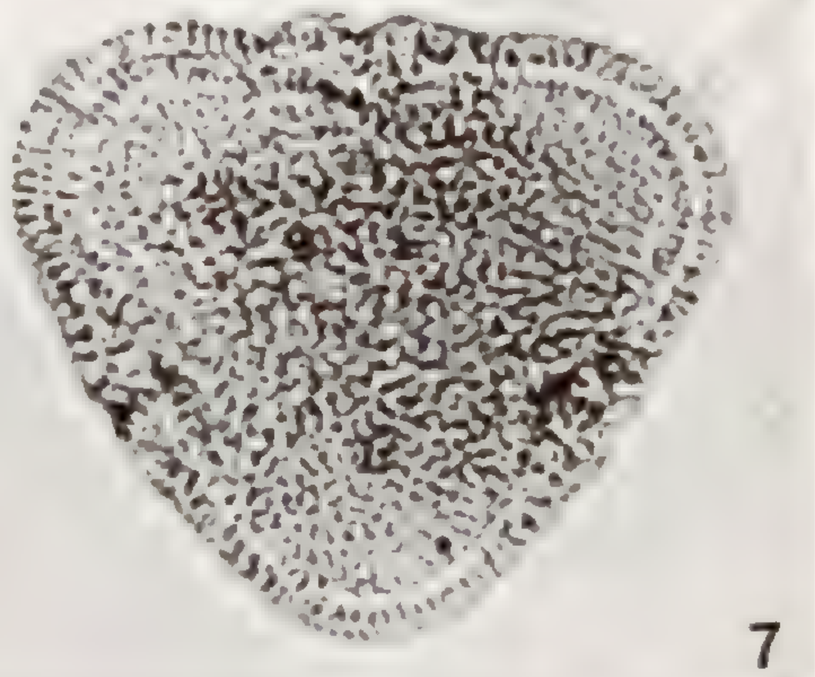
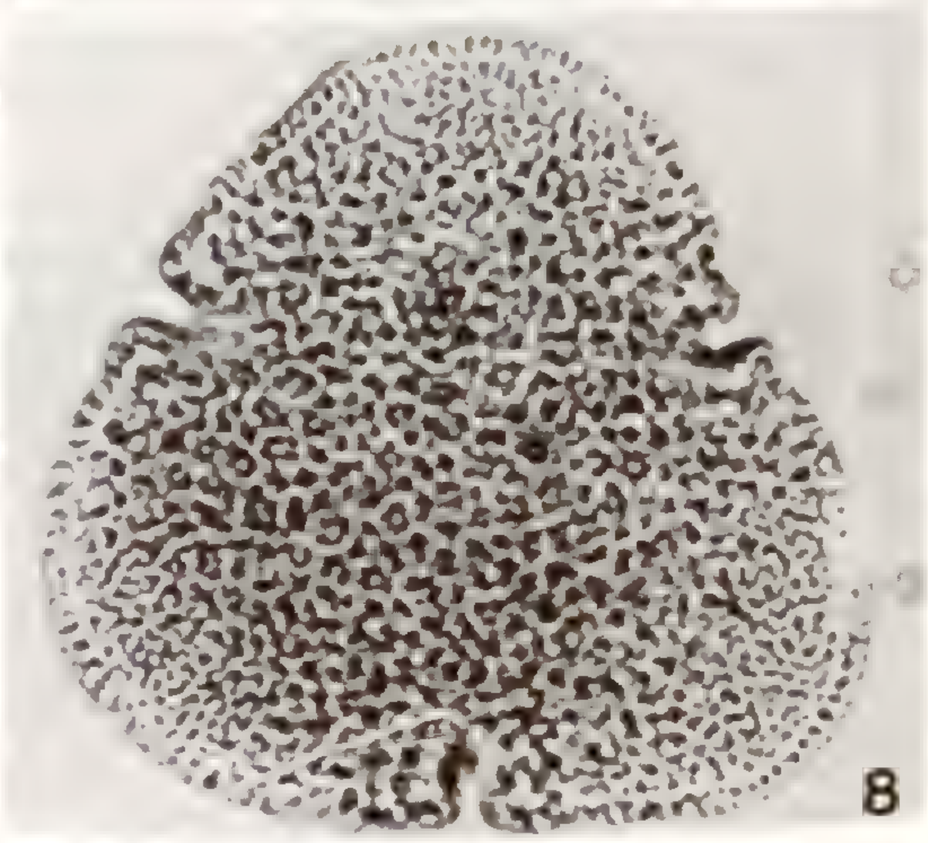












FIGURES 1–8. Fossil pollen from the Gatun Formation.—1, 2. *Cymbopetalum*, SL-103, 253′, 16, ESF N-26; SL-103, 253′, 9, ESF J-29.—3. *Ilex*, SL-103, 253′, 5, ESF E-18.—4, 5. *Combretum/Terminalia*, SL-103, 253′, 7, ESF D-18.—6. cf. *Aguiaria*, SL-103, 253′, 6, ESF O-40.—7. *Bernoullia*, SL-103, 253′, 9, ESF G-21.—8. *Pseudobombax*, SL-103, 253′, 14, ESF P-44. All photographs taken at 400×; size in microns given in descriptions.

AQUIFOLIACEAE

Ilex (Fig. 3). Oblate-spheroidal, amb oval to circular, tricolporoidate (colpi occasionally obscured by sculpture elements), colpi meridionally elongated, equatorially arranged, equidistant, straight, 18–20 μm long, apices acute, inner margin frequently appearing undulate due to overlying sculpture elements, pore poorly defined, frequently obscure, situated at midpoint of colpus; intectate, clavate, wall 3–4 μm thick; 32–34 × 29–31 μm.

Ilex is widespread in northern Latin America, occurring in premontane to montane, wet to drier forest habitats.

Pollen of *Ilex* is found in low percentages in all of our Tertiary microfossil assemblages (Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, La Boca, and Paraje Solo formations). Other occurrences are summarized in Graham (1985, 1987).

BOMBACACEAE

cf. Aguiaria (Fig. 6). Oblate to peroblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, situated in interapical area, short (6–8 μm apex to equator), costae colpi 3–4 μm wide; finely reticulate (diameter of lumen 1 μm or less); tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 34–36 μm.

Pollen of the Bombacaceae is frequent in low percentages in Gulf/Caribbean Tertiary deposits. Assignment of some types to modern genera is difficult because of overlap with the Sterculiaceae and Tiliaceae, and the occurrence of several fossil forms that do not correspond to the pollen of any modern genus in our reference collection or in the literature (Graham, 1989: 59). The specimens are of the *Aguiaria* type (Tsukada, 1964, pl. VII, figs. 10–14; Nilsson & Robyns, 1986, figs. 7f, g), a monotypic genus of Brazil. Similar specimens are known from the La Boca Formation (Graham, 1989), and a smaller, poorly preserved one from the Uscari Formation (Graham, 1987).

Bernoullia (Fig. 7). Oblate to peroblate, amb triangular, apices rounded; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, situated in interapical area, short (6–8 μm apex to equator), costae colpi 4–5 μm wide; finely reticulate (diameter of lumen 1 μm or less), tectate-perforate, wall 3 μm thick, columellae evident in median section (400× magnification); 43–47 μm.

Bernoullia comprises three species of large, tropical trees distributed from Mexico to South America. The pollen specimens are similar to the pollen of *B. flammea* Oliver of Mexico and Central America. A specimen from the San Sebastian Formation (Graham & Jarzen, 1969, fig. 15) described as *Bernoullia* is different and probably is not *Bernoullia*.

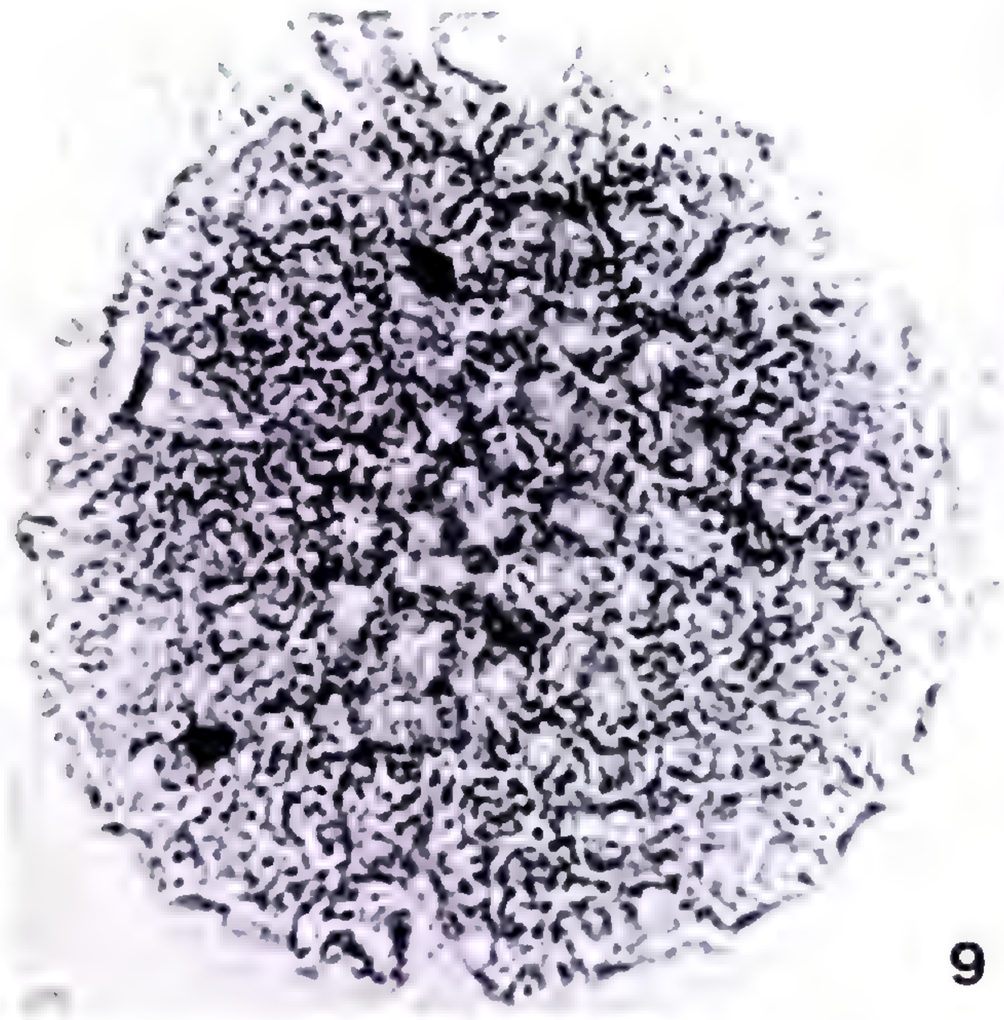
Ceiba (Fig. 9). Oblate to oblate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, short (12–15 μm apex to equator), costae colpi 4–5 μm wide; reticulate, muri narrow (1.5 μm), straight, smooth (appearing beaded from underlying columellae), lumina polygonal, varying in size, larger commonly in polar and mesocolpial areas and 6–8 μm diam., free sexine elements in lumina; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 68–74 μm.

The specimens are similar to pollen of *Ceiba pentandra* (L.) Gaertner, a large pantropical tree occurring in a wide variety of habitats. In Panama it commonly grows in the tropical moist and tropical dry forests, but also in other habitats. Microfossils are known from the La Boca Formation (Graham, 1989, fig. 34, as cf. *Ceiba*).

Pseudobombax (Fig. 8). Oblate to peroblate, amb triangular, apices rounded; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, situated in interapical area, straight, short (8–10 μm), costae colpi 5–6 μm wide; reticulate, muri smooth, narrow (1 μm or less), straight, lumina polygonal, diameter ca. 3 μm in polar area, diminishing to 1 μm or less at apices; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 54–58 μm.

In addition to difficulties noted earlier, the referral of Bombacaceae microfossils to certain modern genera is further complicated by nomenclatural changes among the extant taxa. In particular, *Bombax*, as treated in earlier taxonomic literature, included New World species. Herbarium material, pollen reference collections based on this material, and subsequent reports of microfossils from the Americas as *Bombax*, are frequent in the literature. Robyns (1964; Nilsson & Robyns, 1986: 6), however, placed species of *Bombax* in *Pseudobombax*, *Bombacopsis*, and other genera, with *Bombax* considered an Old World, primarily African, genus. The Gatun specimens are similar to pollen of such species as *Bombax ellipticum* HBK in our reference collection (*Barkley 17M103*, Mexico, TEX), now treated as *Pseudobombax ellipticum* (HBK) Dugand.

In Central America *Pseudobombax* is represented by *P. septenatum* (Jacq.) Dugand, distributed from Nicaragua to Brazil and Peru. In Panama it occurs typically in the tropical moist forest, but is also known from tropical wet, tropical dry, and premontane moist forests (Croat, 1978: 591). Similar pollen occurs in the San Sebastian (Graham & Jarzen, 1969, fig. 22, as *Bombax*), and the La Boca (Graham, 1989, fig. 35) formations.



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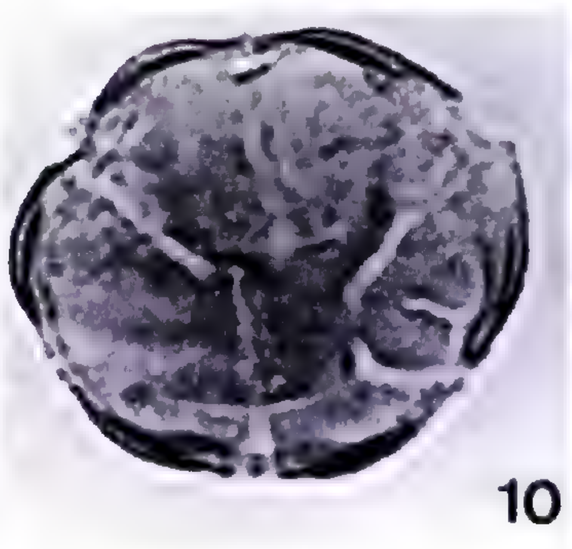

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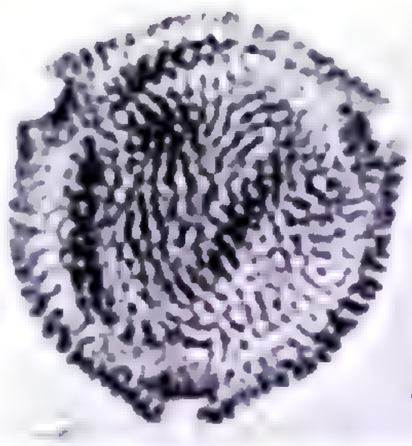

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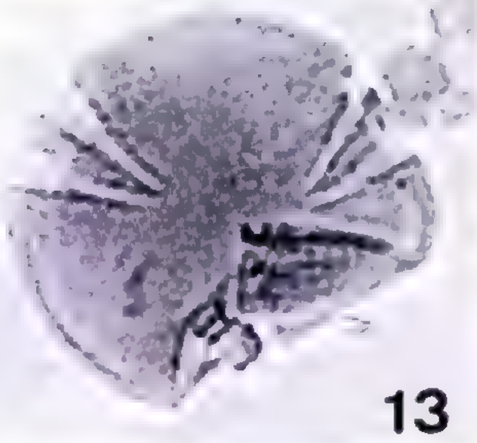

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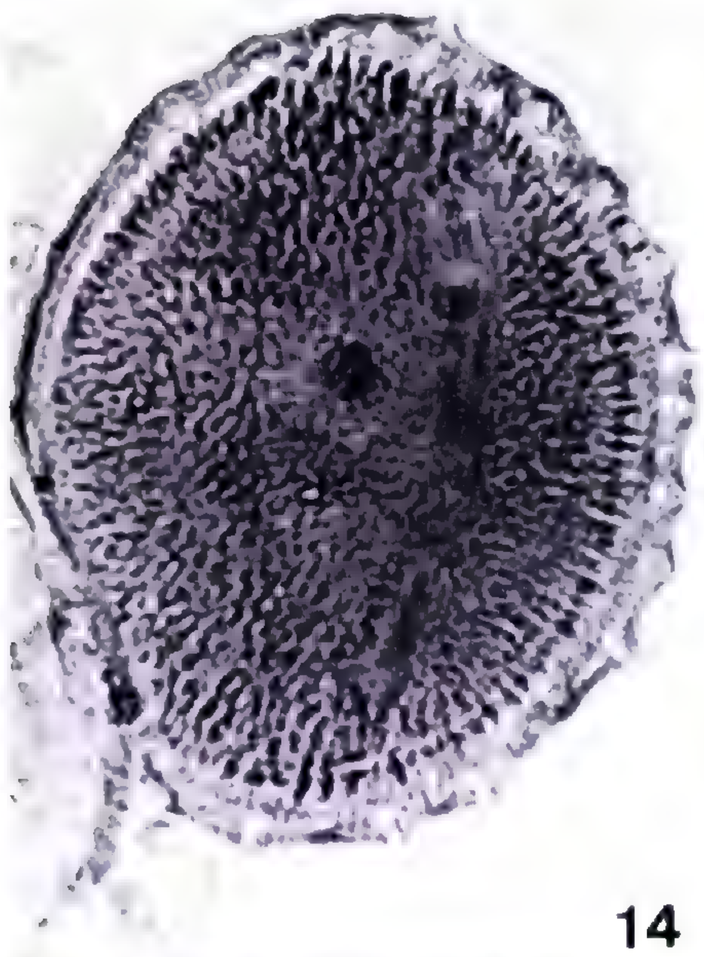

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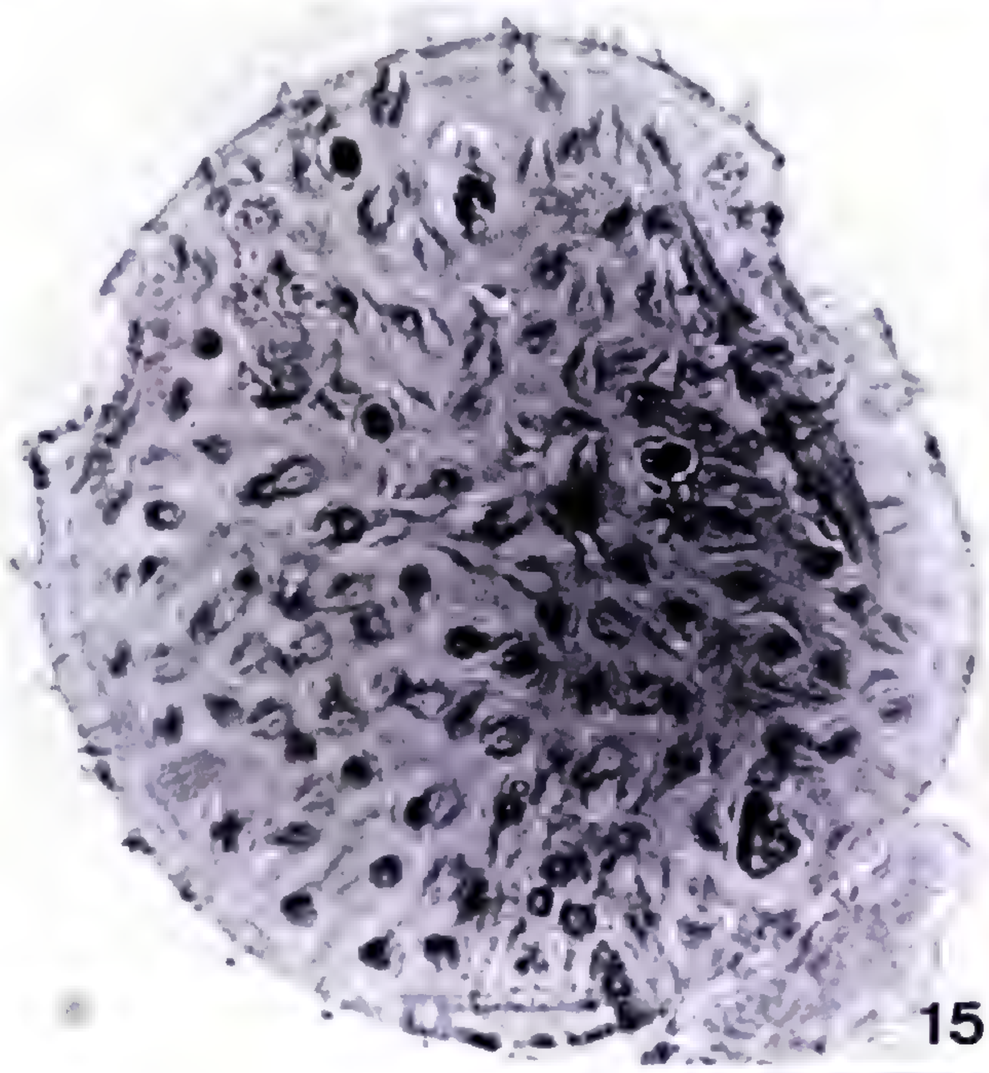

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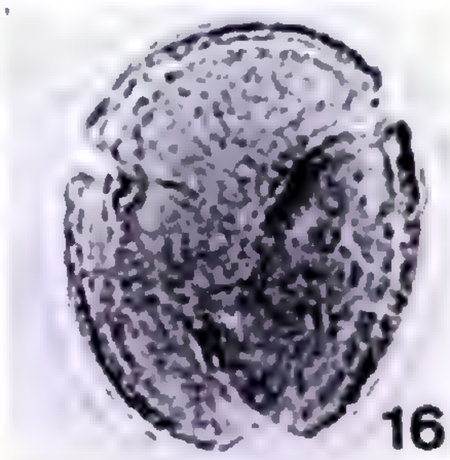

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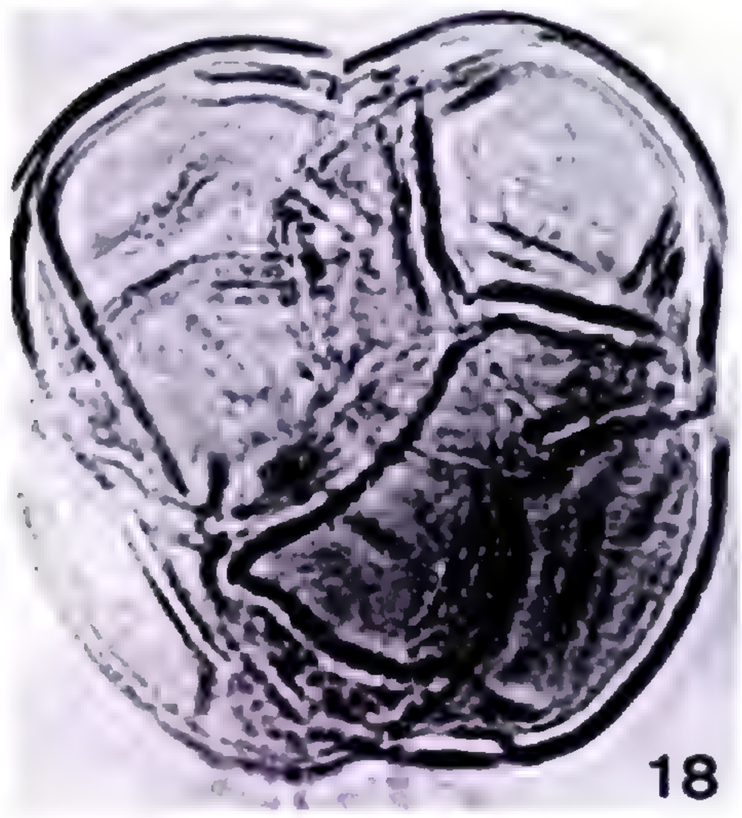

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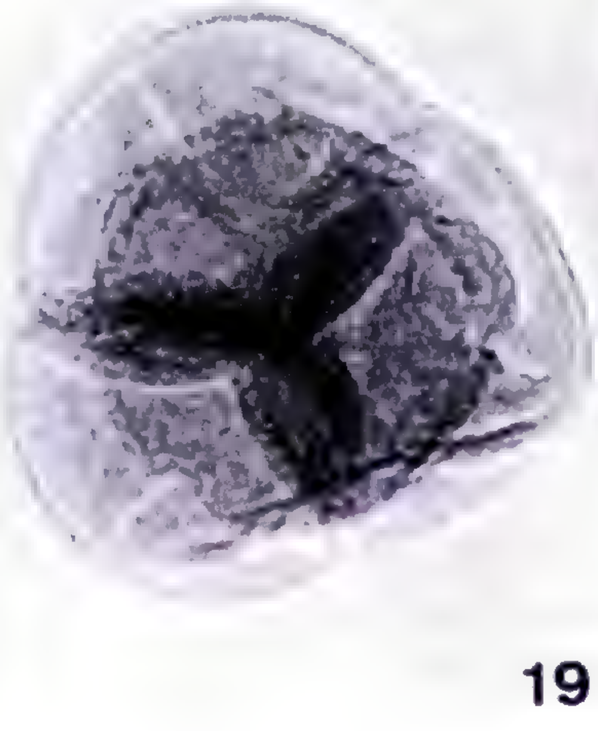

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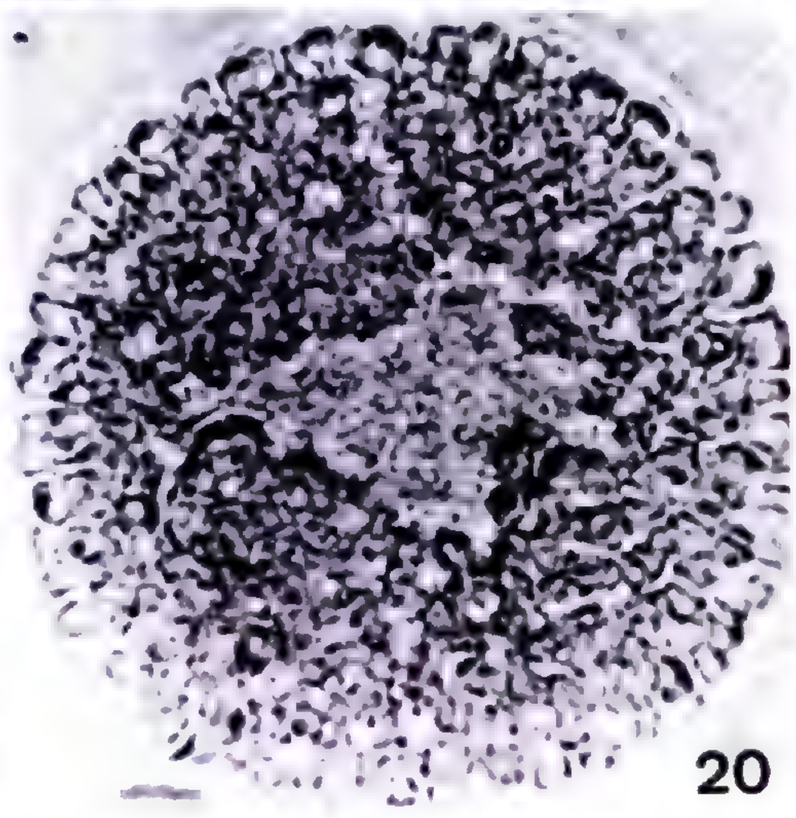

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FIGURES 9–20. Fossil pollen from the Gatun Formation.—9. *Ceiba*, SL-103, 253′, 8, ESF D-41.—10, 11. *Bucida*, SL-103, 253′, 6, ESF G-25; SL-103, 253′, 1. ESF M-39.—12. *Bursera*, SL-103, 253′, 6, ESF V-49.—13. *Alchornea*, SL-103, 253′, 1, ESF T-47.—14. Mutisieae type, SL-103, 253′, 14, ESF J-35.—15. cf. *Cionosicys*, SL-103, 253′, 4, ESF J-21.—16. *Quercus*, SL-103, 253′, 9, ESF L-47.—17. *Alfaroa/Oreomunnea*, SL-103, 253′, 9, ESF R-39.—18, 19. Ericaceae, SL-103, 253′, 5, ESF N-26; SL-103, 253′, 10, ESF K-45.—20. cf. *Jatropha*. SL-103, 253′, 1, ESF X-34.

BURSERACEAE

Bursera (Fig. 12). Oblate-spheroidal, amb oval-triangular to nearly circular; triporate, pores equatorially arranged, equidistant, circular to slightly elongated equatorially, 3–4 μm diam., faint costae pori; striato-reticulate; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 28–30 μm.

Modern pollen of the Mexican species of *Bursera* has been studied by Palacios Chávez (1984). The fossil specimens are similar to *B. simaruba* (L.) Sarg. et al., a tree or shrub of widespread distribution from southern Florida, through Mexico and the Antilles, to Colombia, Venezuela, and the Guianas. It is typical of the tropical moist forest, but also occurs in tropical wet, tropical dry, premontane moist, and premontane dry forests. *Bursera* pollen is known from the San Sebastian (Graham & Jarzen, 1969, fig. 23) and Paraje Solo (Graham, 1976, figs. 63, 64) formations.

COMBRETACEAE

cf. Bucida (Figs. 10, 11). Prolate-spheroidal, amb circular, lobate due to thinning of wall at apertures; tricolporate with three pseudocolpi, colpi equatorially arranged, meridionally elongated, equidistant, straight, ca. 15 μm long (apex to equator), colpus margin entire to slightly dentate, pseudocolpi similar, slightly shorter (ca. 12 μm apex to equator), pores circular, 3 μm diam., situated at midpoint of colpus; scabrate; tectate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 30 μm.

Bucida is a genus of four species distributed from southern Florida to Central America and the Antilles. One species, *B. buceras* L., is listed for Panama (D'Arcy, 1987), a small tree or shrub growing in wet forests and strand thickets at elevations from sea level to about 1,000 m. It has been reported as a megafossil from the Eocene Wilcox Formation of Kentucky (Berry, 1941) and from the Tertiary of the Dominican Republic (Berry, 1921); however, these megafossil records have not been reevaluated using modern methods of foliar architecture and cuticular anatomy. As a microfossil it is known only from the Gatun Formation. Similar scabrate, tricolporate grains with three pseudocolpi occur in several families of the Myrtales (Combretaceae, Lythraceae, Melastomataceae); hence, the provisional cf. identification.

Combretum/Terminalia (Figs. 4, 5). Prolate-spheroidal, amb circular, lobate in polar view; heterocolpate, colpi three, equatorially arranged, meridionally elongated, equidistant, straight, 8–10 μm long (apex to equator), colpus membrane faintly and minutely granular, margin entire to slightly diffuse, pores faint, situated at midpoint of colpus, 3–4 μm diam., pseudocolpi three, alternating with colpi, slightly shorter (6–8 μm); psilate; tectate, wall 3 μm thick, wall homogeneous (400× magnification); 18–24 μm.

Pollen of the Combretaceae was surveyed to determine the possibility of distinguishing between the common tropical trees *Combretum* and *Terminalia* (Graham, 1980). Pollen of the two genera could not be distinguished consistently, especially in the limited numbers encountered in the dispersed state, and the microfossils are referred to *Combretum/Terminalia*. *Combretum* is widespread in the New and Old World tropics, with about seven species in Panama. It commonly grows as a coastal or shore plant in tropical wet, tropical moist, premontane wet, and premontane moist forests. *Terminalia* is also widespread and is represented in Panama by about nine species, typically growing in tropical wet, tropical moist, premontane wet, and premontane moist forests. Microfossils are known from the Gatuncillo, Culebra, and Paraje Solo formations.

COMPOSITAE

Mutisieae type (Fig. 14). Prolate to prolate-spheroidal; tricol(por?)ate (pores obscure), colpi equatorially arranged, meridionally elongated, equidistant, ca. 45–48 μm long; echinate, echinae ca. 2 μm long, broad at base, tectate, wall 8–9 μm thick, individual columellae and two wall layers evident in median section (400× magnification), inner wall 4–5 μm thick, outer wall (including ca. 2-μm spines) 3–4 μm thick; 68 × 60 μm.

Among the pollen types surveyed in our reference collection and in the literature, this specimen most closely resembles *Mutisia*. However, this is a South American genus of high altitudes and/or arid habitats, and these conditions are not known to have existed in southern Central America during the Tertiary. Because the survey of modern genera of the Mutisieae is not complete, the specimen is provisionally referred only to the Mutisieae type of pollen.

CUCURBITACEAE

cf. Cionosicys (Fig. 15). Spherical, amb circular; triporate, pores equatorially arranged, equidistant, circular, large (12–15 μm), inner margin entire; surrounded by faint, granular costae pori 3

μm wide; echinate, echinae 3–4 μm long, broadening at base, surface between echinae faintly scabrate; tectate, wall thin (3 μm) in relation to size of grain, frequently folded, individual columellae just visible in median section (400× magnification); 88–94 μm.

The Cucurbitaceae are eurypalynous (Ayala-Nieto et al., 1988; Campos, 1962; Dieterle, 1976; Marticorena, 1963; Melhem, 1966), and although several genera have large, echinate pollen grains, many of these are periporate. The Gatun specimens are similar to the triporate pollen of *Cionosicys*, but differ in that the spines are not as robust, hence the cf. identification. *Cionosicys* is a Caribbean genus of three species with one [*C. macranthus* (Pittier) C. Jeffery] in Panama. The plant is a large vine growing in moist forests and open thickets, often along streams from Mexico to Panama (Wunderlin, 1978).

The Cucurbitaceae are poorly represented in the Gulf/Caribbean microfossil record. Probably because of their large, relatively fragile pollen produced in small amounts, and their entomophilous pollination. The oldest pollen record for the family is from the Oligocene of Cameroon (Muller, 1981: 39). The family has not been reported previously from the Gulf/Caribbean Tertiary, although some large ornate forms reported as unknowns (e.g., Fig. 85) may belong to the Cucurbitaceae. Bartlett & Barghoorn (1973) reported a different form as *Sechium edule*-type pollen from Quaternary deposits in Panama.

ERICACEAE

Type 1 (Fig. 18). Tetrahedral tetrad; individual grains spherical (compressed in tetrad), amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, inner margin entire, colpi shared (continuous across contact between grains); scabrate; tectate, wall 2 μm thick, homogeneous (400× magnification); individual grains 30–34 μm, tetrad ca. 50 μm.

Type 2 (Fig. 19). These grains are similar to type 1, but are smaller. The individual grains are 25–28 μm diam. and the tetrads are 35–40 μm.

The occurrence of Ericaceae pollen in Gulf/Caribbean Tertiary deposits has been discussed by Graham (1987: 1511). Briefly, the specimens cannot be identified to genus, but the larger grains fall within the range of variation of *Cavendishia*, a large genus of about 150 species of epiphytic and terrestrial shrubs distributed from southern Mexico through Central America into South America as far as Bolivia. About 30 species are recognized for Panama, where they are most common at moderate to higher altitudes. Ericaceae pollen has been reported previously from the Uscari Formation.

EUPHORBIACEAE

Alchornea (Fig. 13). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 10–12 μm long, extending within 5 μm of pole, inner margin entire, distinct operculum 3 μm wide; faintly scabrate; tectate, wall 2 μm thick, homogeneous to columellae occasionally just visible in median section (400× magnification); 26–30 μm.

Alchornea is widespread in the Neotropics, represented by about eight species in Panama. It grows in tropical moist, premontane wet, and premontane rainforests at altitudes from about 300 to 2,000 m. *Alchornea* is frequently present in low percentages in Gulf/Caribbean Tertiary microfossil floras (San Sebastian, Uscari, Culebra, Cucaracha, La Boca, and Paraje Solo formations).

cf. Glycydendrum (Figs. 21, 22). Oblate to oblate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 8–10 μm long, inner margin entire to minutely lobate; clavate, clavae fine, ca. 2 μm long; intectate, wall 2–3 μm thick; 42–45 μm.

Glycydendrum is one of the few genera presently confined to South America (Amazonian Brazil) that appears to be represented in southern Central American Tertiary deposits. Similar pollen occurs

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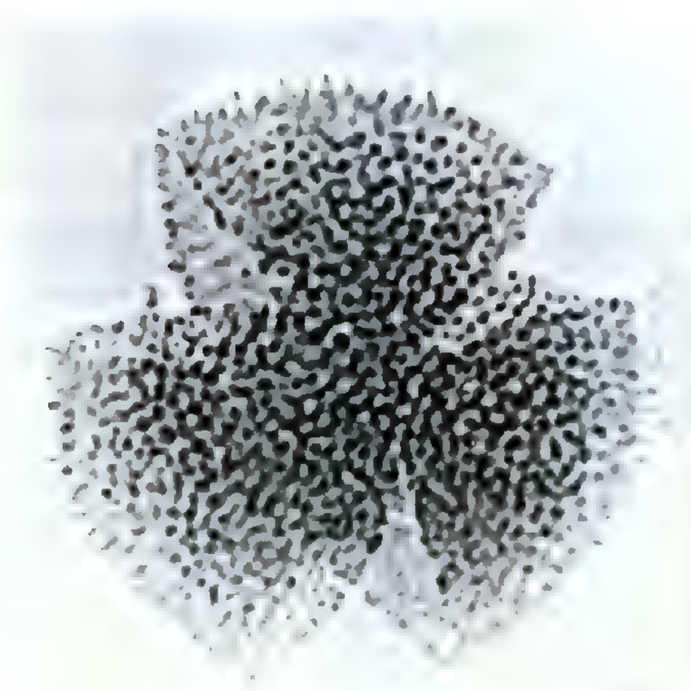
FIGURES 21–35. Fossil pollen from the Gatun Formation.—21, 22. *Glycydendrum*, SL-103, 253′, 8, ESF S-34; SL-103, 253′, 2, ESF K-22.—23. cf. *Stillingia*, SL-103, 253′, 14, ESF C-40.—24. *Acacia*, SL-103, 257′, 3, ESF K-27.—25. *Crudia*, SL-103, 253′, 11, ESF J-45.—26. *Erythrina*, SL-103, 253′, 4, ESF N-20.—27. Melastomataceae, SL-103, 253′, 2, ESF G-28.—28. *Eugenia/Myrcia*, SL-103, 253′, 1, ESF K-37.—29. *Rhizophora*, SL-103, 253′, 7, ESF E-14.—30. *Utricularia*, SL-103, 253′, 12, ESF M-31.—31. Loranthaceae type 1, SL-103, 253′, 8, ESF R-51.—32. Loranthaceae type 2, SL-103, 253′, 7, ESF D-33.—33. Malpighiaceae type 2, SL-103, 253′, 4, ESF V-24.—34. Malpighiaceae type 1, SL-103, 253′, 9, ESF J-21.—35. *Cedrela*, SL-103, 253′, 1, ESF F-52.



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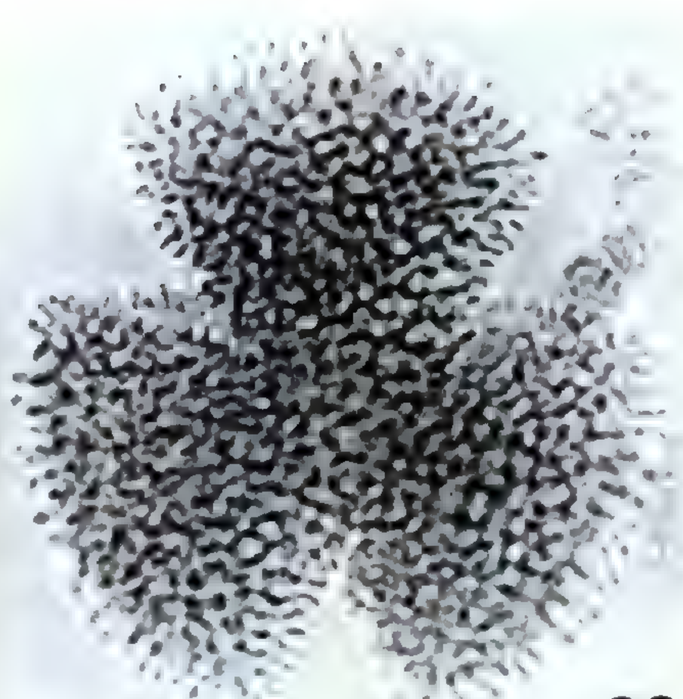

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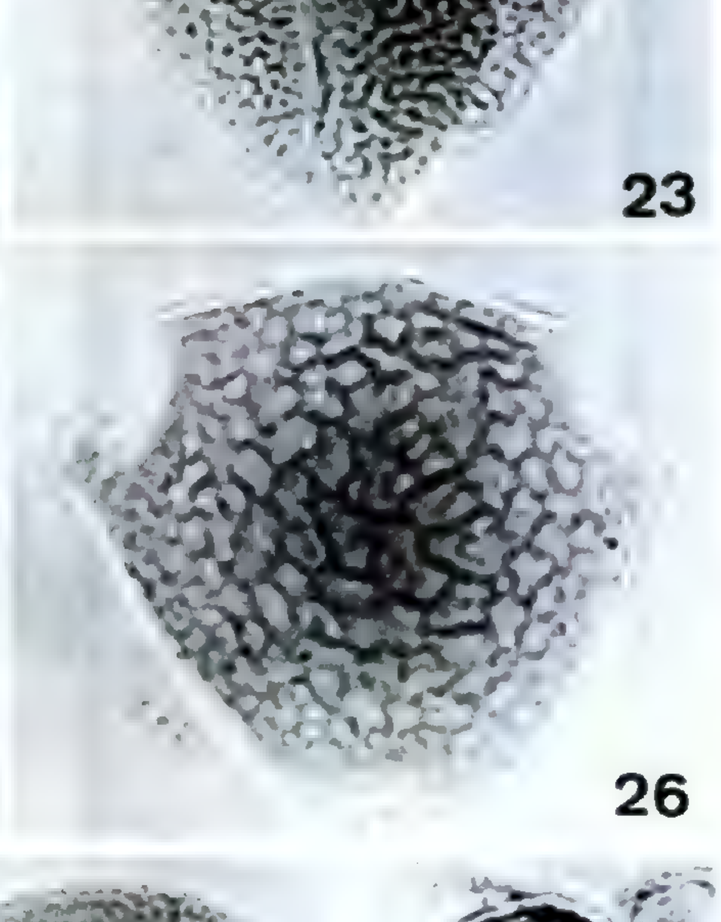

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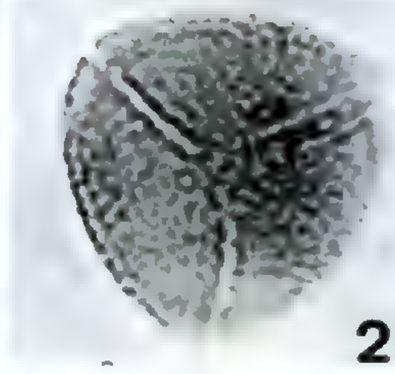

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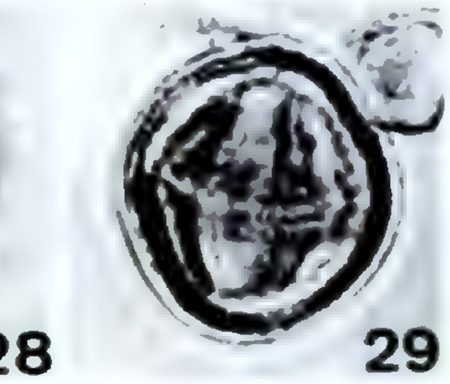

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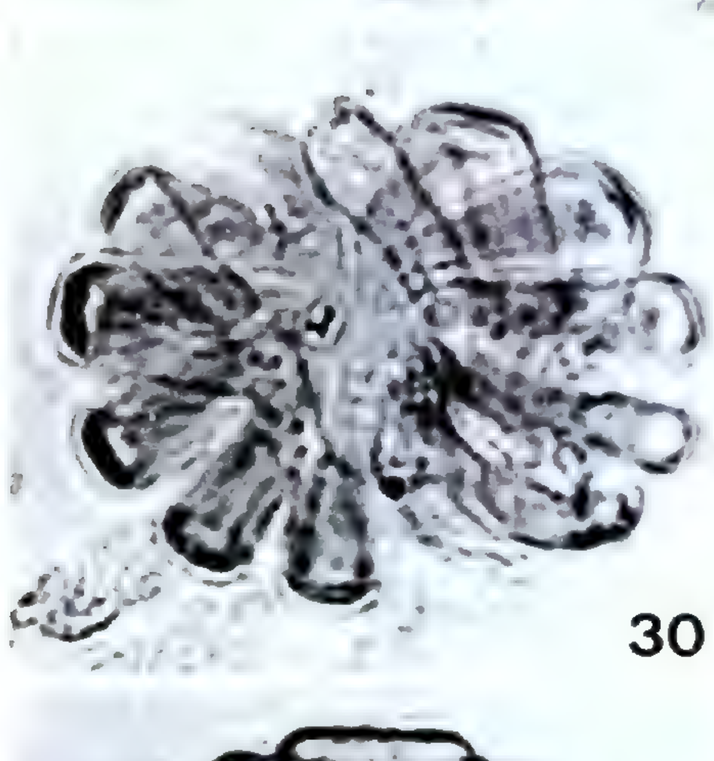

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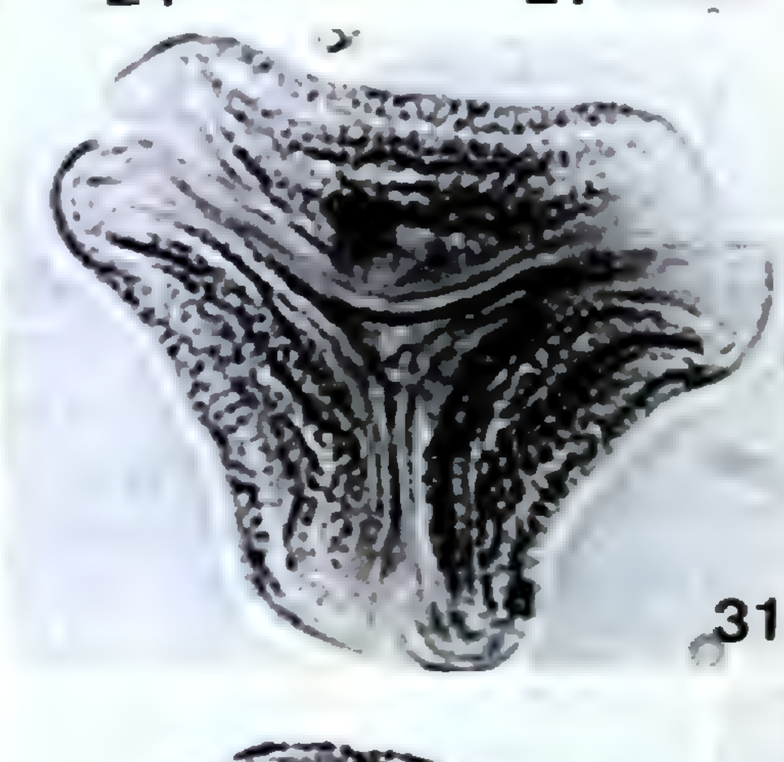

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in *Tetrorchidium*, but the columellae in that genus are finer and nearly echinate. *Glycydendrum*-type pollen is present in the Uscari Formation, and Bartlett & Barghoorn (1973) reported *Glycydendrum* from Quaternary deposits in Gatun Lake, Panama.

cf. Jatropha (Fig. 20). Spherical, amb circular; nonaperturate; intectate, clavate, clavae relatively large and coarse, 3 × 4 μm, frequently triangular in outline; wall 4 μm thick; 56–60 μm.

The specimens have the wedge shape or triangular clavae typical of many Euphorbiaceae (e.g., *Croton, Manihot*), but these are not arranged into the stellate clusters or "crotonoid" pattern of these genera. The specimens cannot be identified below the level of family but are similar to pollen of *Jatropha*. The genus is widespread in Latin America, and four species are recorded for Panama. The plants range from the tropical moist forest to drier vegetation types. This type of Euphorbiaceae pollen has not been reported previously from Gulf/Caribbean Tertiary deposits.

cf. Stillingia (Fig. 23). Prolate, amb oval; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 59–62 μm long, inner margin entire, pore situated at midpoint of colpus, equatorially elongated, 2 × 4–5 μm; finely reticulate, lumina ca. 1 μm diam.; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 68–72 × 49–51 μm.

These large, prolate, triangular, reticulate grains are similar to *Stillingia*, a primarily New World tropical genus of 25–30 perennial herbs, shrubs, or small trees (Webster & Burch, 1967). The genus is represented in Panama by *S. zelayensis* (HBK) Muell.-Arg., which produces pollen similar to the Gatun specimens. *Stillingia* has been reported previously from the Paraje Solo Formation (as cf. *Stillingia*; Graham, 1976, fig. 114).

FAGACEAE

Quercus (Fig. 16). Prolate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 15–18 μm long, inner margin entire; scabrate; tectate, wall 2 μm thick, homogeneous; (400× magnification); 38 μm.

This is the earliest record of *Quercus* in Tertiary deposits of southern Central America, and it is rare in these Gatun sediments. It was more abundant in the Pliocene Paraje Solo Formation of Veracruz, Mexico, and first appeared in South America about 900,000 years ago (van der Hammen in Livingstone & van der Hammen, 1978). It was not recorded from Gatun Lake Quaternary deposits in Panama (Bartlett & Barghoorn, 1973), but was present in late Quaternary sediments from west coastal Costa Rica (Horn, 1985). Thus, the north-to-south migration of *Quercus* during the Tertiary and its relatively recent introduction into southern Central America and particularly South America (late Quaternary) seems clear, based on present data (Crepet & Nixon, 1989).

JUGLANDACEAE

Alfaroa/Oreomunnea (Fig. 17). Oblate, amb circular; triporate, pores equatorially arranged, equidistant, circular, 3–4 μm diam., inner margin entire; psilate to faintly scabrate; tectate, wall 2 μm thick, homogeneous (400× magnification); 27–30 μm.

Englehardia sensu lato was earlier considered a component of warm temperate vegetation in both the New and Old Worlds. Following the treatment of Stone & Broome (1975), however, *Englehardia* is now treated as an Old World genus, with related taxa in the New World assigned to *Alfaroa* and *Oreomunnea*. *Alfaroa* is a genus of about seven species growing in the highlands of Mexico, Central America, and northern Colombia. *Oreomunnea* comprises two species, "one ranging from the premontane cloud forests of southern Mexico to central Costa Rica (*O. mexicana* with two subspecies) and the other (*O. pterocarpa*) endemic to the Río Reventazón Valley of central Costa Rica" (Stone & Broome, 1975: 2).

Alfaroa/Oreomunnea-type pollen is known in the stratigraphic literature as *Momipites* and is present in the Gatuncillo, San Sebastian, Cucaracha, La Boca, and Paraje Solo formations. It is also reported from the Oligo–Miocene Simojovel Group of Chiapas, Mexico (Langenheim et al., 1967). The fossil record of the Juglandaceae, including *Alfaroa* and *Oreomunnea*, has been summarized by Manchester (1987).

LEGUMINOSAE

Mimosoideae

Acacia (Fig. 24). Sixteen-cell polyad; individual grains square to polygonal (compressed in polyad); nonaperturate, psilate to faintly scabrate; tectate, wall 2 μm thick, homogeneous to minute columellae just visible in median section (400× magnification); individual grains ca. 30 μm, polyad 120 × 88 μm (broken).

Twelve species of *Acacia* are found in Panama (fide Woodson & Schery, 1950), and five are listed for Barro Colorado Island (Croat, 1978). They are common in the tropical moist forest, but range into more open, drier habitats. *Acacia* pollen occurs in the San Sebastian, Culebra, and Paraje Solo formations.

Caesalpinioideae

Crudia (Fig. 25). Prolate; tricolporoidate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 30–35 μm long, extending nearly entire length of grain, pore area faint, circular, situated at midpoint of colpus; distinctly and coarsely striate, striae generally oriented parallel to long axis of grain, surface of striae psilate, margin entire, occasionally appearing beaded from underlying pores in foot layer/endexine; tectate but with occasional separation between sculpture elements, wall 2 μm thick, homogeneous (400× magnification); 44–48 × 28–32 μm.

Pollen of the Caesalpinioideae, including *Crudia*, has been studied by Graham & Barker (1981). *Crudia* is a South American, mainly Amazonian, genus of about 10 mostly riverine species. It is recorded in the stratigraphic literature as *Striatocolpites cataumbus* and in northern Latin America is known from the Gatuncillo, Cucaracha, and La Boca formations. Herendeen & Dilcher (1988) reported *Crudia*-type pods from the Eocene of western Tennessee.

Papilionoideae

Erythrina (Fig. 26). Oblate, amb oval-triangular; triporate, pores equatorially arranged, equidistant, circular (10–12 μm, compressed open), inner margin entire, surrounded by narrow margo ca. 4–5 μm wide formed by diminution of sculpture bordering pores; reticulate, muri thin (1 μm), low, smooth, sinuous, lumina polygonal, ca. 6–7 μm diam. in polar area, becoming finer toward equator and especially toward pores; tectate, wall 2–3 μm thick, homogeneous (400× magnification); 34–37 μm.

Pollen of the Erythrineae has been studied by Graham & Tomb (1974, 1977). This type of *Erythrina* pollen is produced by several Central American species, including *E. caribeae* Krukoff & Barneby, *E. castillejiflora* Krukoff & Barneby, *E. chiriquensis* Krukoff, *E. cobanensis* Krukoff & Barneby, *E. fusca* Loureiro, *E. guatemalensis* Krukoff, *E. williamsii* Krukoff & Barneby, and others. The plants occur through a wide range of habitats, including tropical wet, tropical moist, and premontane rainforests, from low to moderate elevations. *Erythrina fusca* sometimes forms pure stands in freshwater marshes (Holdridge, 1970 in Croat, 1978: 473).

LENTIBULARIACEAE

Utricularia (Fig. 30). Oblate-spheroidal, amb circular; stephanocolpate, colpi equatorially arranged, meridionally elongated, equidistant, ca. 15–18 μm long (apex to equator), 12 in number, inner margin entire; psilate; tectate, wall 2–3 μm thick, homogeneous (400× magnification); 42–45 μm.

Sixteen species of *Utricularia* are listed for Panama (D'Arcy, 1987), with two (*U. foliosa* L.; *U. obtusa* Sw.) occurring in the waters surrounding Barro Colorado Island. It is a freshwater, perennial, stoloniferous herb of widespread distribution from temperate to tropical regions in both the New and Old Worlds. Pollen has been reported from the Miocene of Senegal (Médus, 1975), and from the Pliocene Paraje Solo Formation of Mexico (Graham, 1976).

LORANTHACEAE

Type 1 (Fig. 31). Oblate, amb concavo-triangular, apices blunt; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 25–27 μm long (pole to apex), syncolpate, inner margin entire; mesocolpium baculate to slightly echinate, becoming psilate at apices; intectate in mesocolpium, tectate at apices, wall 1.5 μm thick, tectate portion homogeneous (400× magnification); 42–46 μm.

Type 2 (Fig. 32). Oblate, amb concavo-triangular, apices rounded; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 23–25 μm long (pole to equator), syncolpate, inner margin entire; finely striate with minute echinae between striae; tectate, wall 1.5 μm thick, homogeneous; 34–36 μm.

Both specimens are of the Loranthaceae type but cannot be referred to any one modern genus. Type 1 is generally similar to *Aetanthus*, and type 2 to *Psittacanthus*. Modern neotropical Loranthaceae pollen has been studied by Feuer & Kuijt (1979, 1980, 1985), and fossil pollen has been reported previously from the San Sebastian and Paraje Solo formations.

MALPIGHIACEAE

Type 1 (Fig. 34). Oblate-spheroidal, amb circular; periporate with colpal arcs connecting pores, pores circular, 4–6 μm diam., inner margin entire,

inner margin of colpal arc minutely dentate, occasional free sexine elements on colpal membrane; scabrate; tectate, wall 3–4 μm thick, individual columellae evident in median section (400× magnification); 36–38 μm.

Type 2 (Fig. 33). Oblate-spheroidal, amb circular; periporate with colpal arcs connecting pores, pores circular, 3 μm diam., inner margin entire, inner margin of colpal arc minutely dentate, occasional free sexine elements on colpal membrane; scabrate, with occasional larger, low verrucae; tectate, wall 4–5 μm thick, homogeneous (400× magnification); 44–46 μm.

The Malpighiaceae are frequent in Gulf/Caribbean Tertiary deposits, but in low percentages. Although the family is moderately eurypalynous, most fossil pollen cannot be referred consistently to any one modern genus. Malpighiaceae pollen has been reported previously from the Gatuncillo, Uscari, Culebra, La Boca, and Paraje Solo formations.

MALVACEAE

Hampea/Hibiscus (Fig. 36). Spherical, amb circular; periporate, pores circular, 3–4 μm diam., inner margin entire; echinate, echinae 5–7 μm long, occasionally curved, broad at base, surface between echinae scabrate; tectate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 75 μm (excluding spines).

There is sufficient overlap in the pollen of *Hampea* and *Hibiscus* that individual dispersed microfossils cannot be referred consistently to one genus. *Hampea* is represented in Panama by six species (D'Arcy, 1987), including the common *H. appendiculata* (J. D. Smith) Standley, which also occurs in Honduras and Costa Rica. It is a shrub to mid-size tree of tropical wet, tropical moist, premontane rain, and premontane moist forests. *Hibiscus* is represented by 12 species in Panama, including *H. sororius* L.f., a species common in marshy areas and coastal strand vegetation. Similar specimens have been recovered from the Culebra and Paraje Solo formations.

Melastomataceae (Fig. 27). Oblate-spheroidal, amb circular; heterocolpate, tricolporate with three pseudocolpi, colpi equatorially arranged, meridionally elongated, equidistant, straight, 6–7 μm long (apex to equator), inner margin entire, pores obscure, situated at midpoint of colpus, pseudocolpi slightly shorter to as long as colpi; psilate, tectate, wall 2 μm thick, homogeneous (400× magnification); 18–20 μm.

Dispersed fossil pollen of the Melastomataceae cannot be referred to any single modern genus, and in some cases they overlap morphologically with the pollen in other heterocolpate myrtalean families. The specimens serve only to record Melastomataceae-type pollen in Gulf/Caribbean Tertiary deposits. Similar pollen has been recovered from the Uscari and possibly the Culebra (unknown type 5) formations.

MELIACEAE

Cedrela (Fig. 35). Prolate-spheroidal; tetracolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 32–34 μm long, costae colpi 3–4 μm wide, pores situated at midpoint of colpus, slightly elongated equatorially, 4 × 6 μm; psilate; tectate, wall 3 μm thick, homogeneous (400× magnification); 50–52 × 42–44 μm.

The pollen of some species in Flacourtiaceae, Meliaceae, and Sapotaceae is similar and often difficult to separate in the dispersed fossil state. The relatively large (50 μm), tetracolporate specimens are most similar to *Cedrela* in our reference collection. Four species are listed for Panama (D'Arcy, 1987), and two are widespread in northern Latin America. *Cedrela odorata* L. occurs from northern Mexico to South America and the Antilles. In Panama it grows in tropical moist, tropical dry, and premontane wet forests. *Cedrela angustifolia* Sessé & Mociño occurs in the tropical moist and tropical dry forests and is most abundant along the Pacific slope. Both grow at low to moderate elevations. *Cedrela* has been reported previously from the Paraje Solo Formation.

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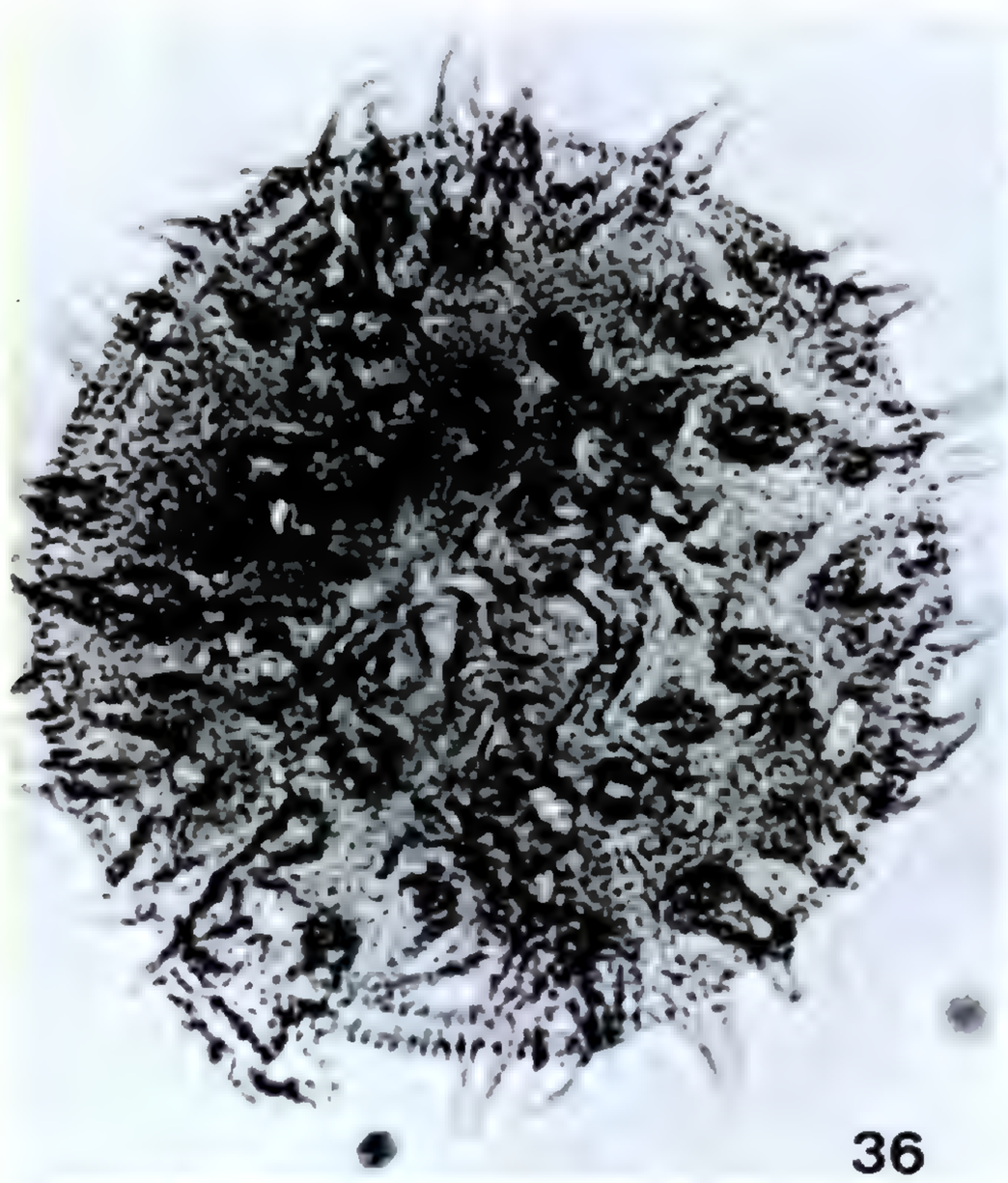
FIGURES 36–50. Fossil pollen from the Gatun Formation.—36. *Hampea/Hibiscus*, SL-103, 253′, 5, ESF N-37.—37. *Hauya*, SL-103, 253′, 14, ESF H-35.—38. *Cabomba*, SL-103, 253′, 1, ESF J-51.—39, 42. *Guarea*, SL-103, 253′, 13, ESF L-39; SL-103, 253′, 6, ESF S-29.—40. *Chomelia* type, SL-103, 253′, 7, ESF F-23.—41. *Faramea*, SL-103, 253′, 7, ESF D-34.—43. *Cosmibuena*, SL-103, 253′, 1, ESF M-44.—44, 45, 48. *Faramea*, SL-103, 253′, 1, ESF H-37; SL-103, 253′, 9, ESF H-20; SL-103, 253′, 2, ESF F-42.—46, 47, 49. *Casimiroa*, SL-103, 253′, 1, ESF P-40; SL-103, 253′, 1, ESF H-43.—50. *Paullinia*, SL-103, 253′, 7, ESF U-45.



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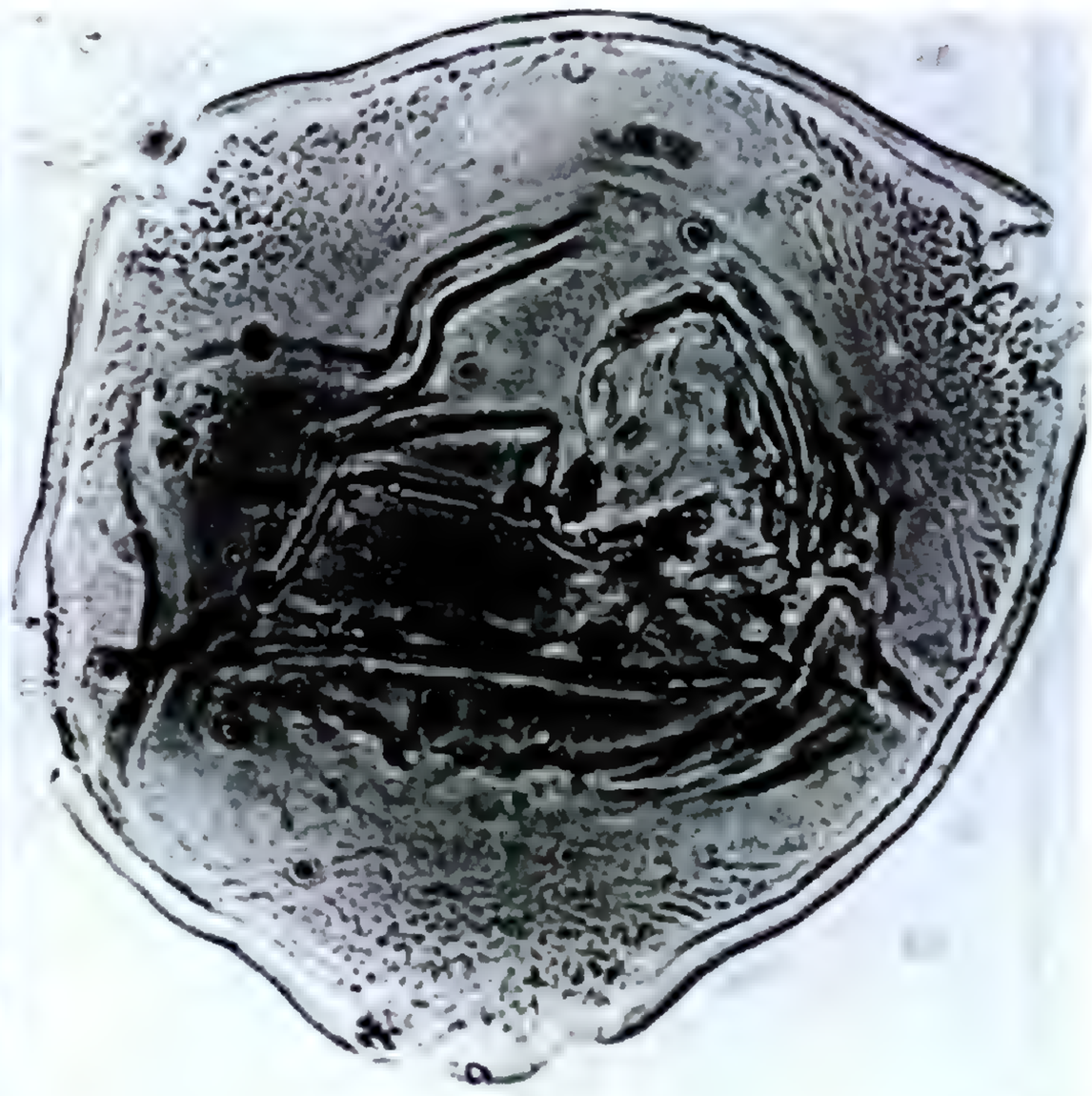

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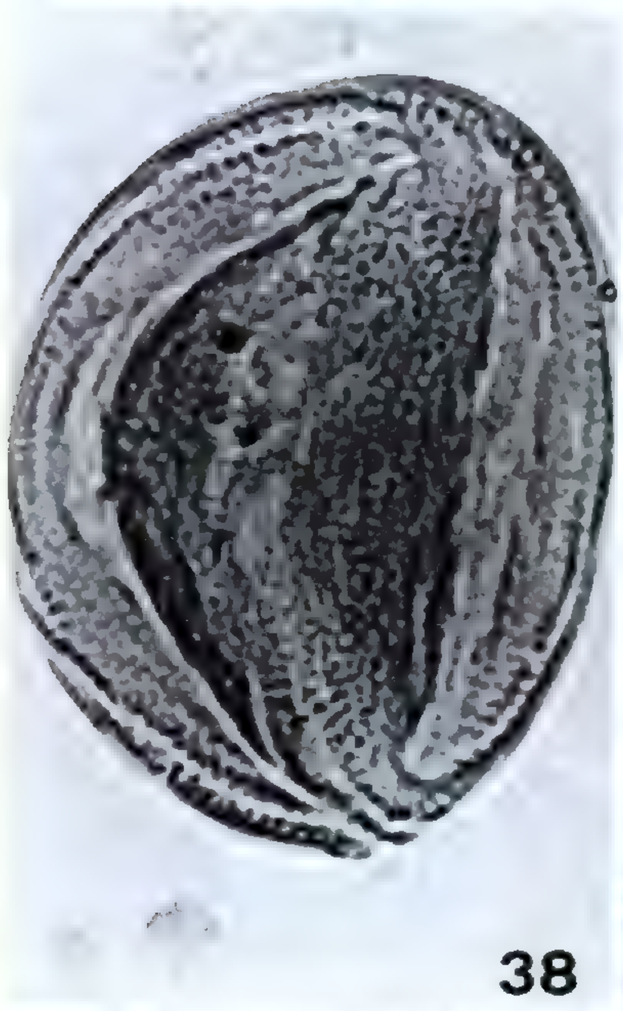

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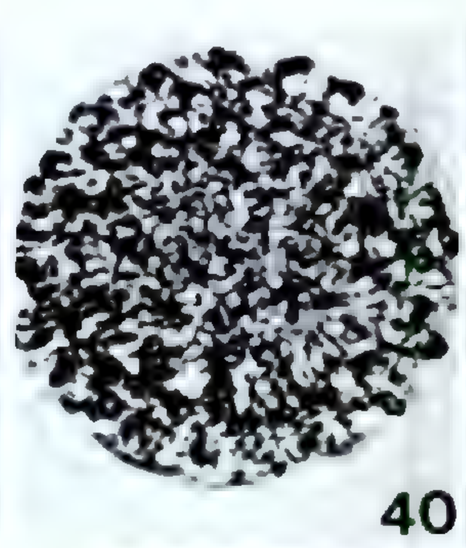

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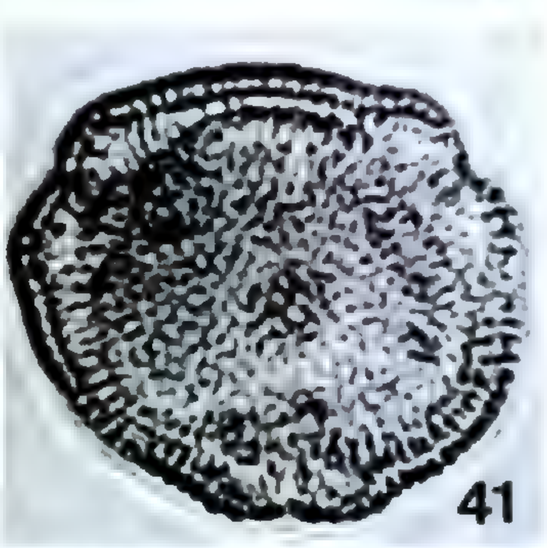

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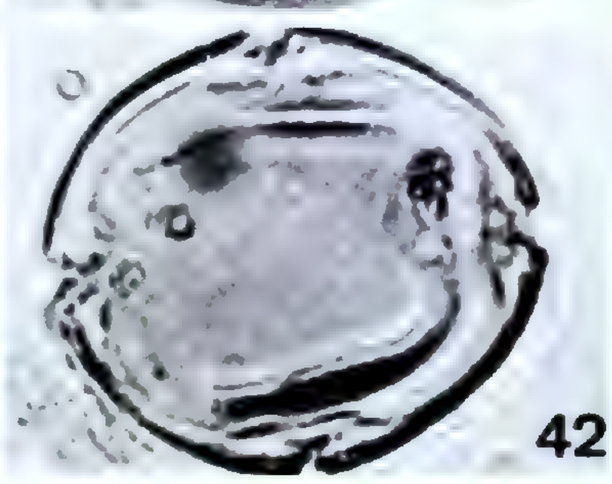

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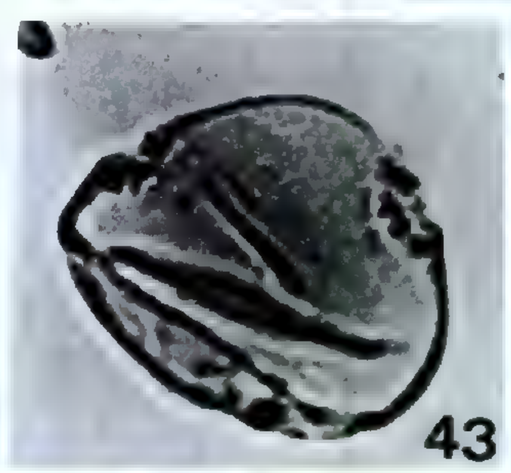

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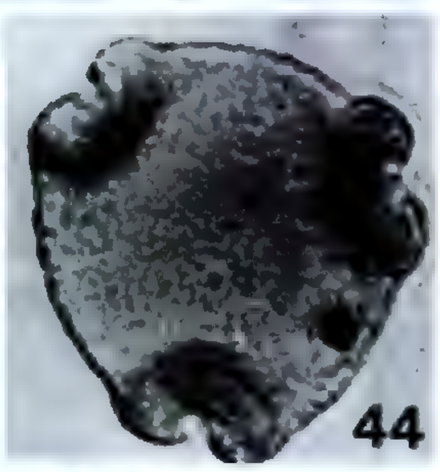

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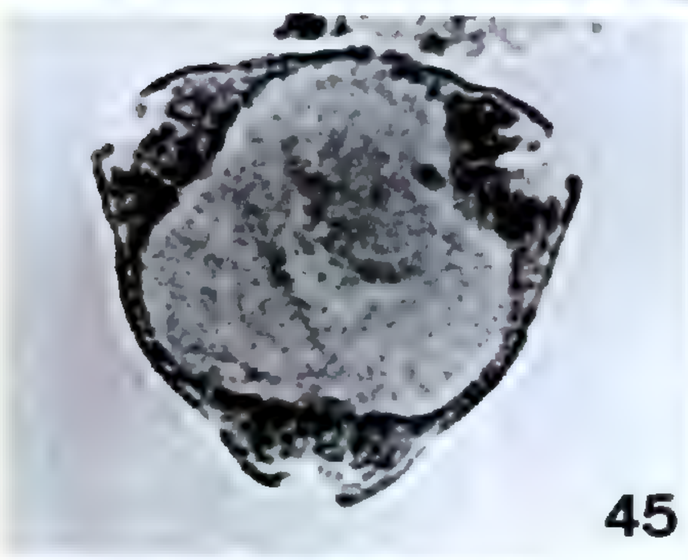

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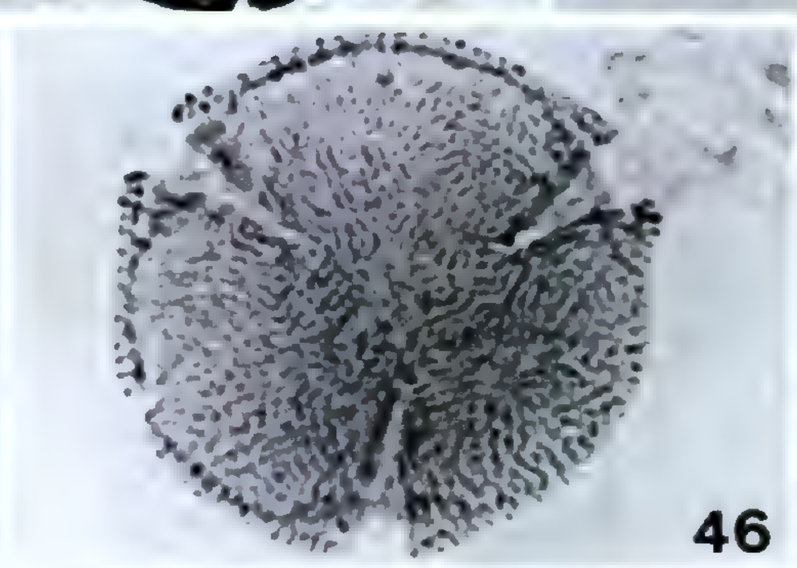

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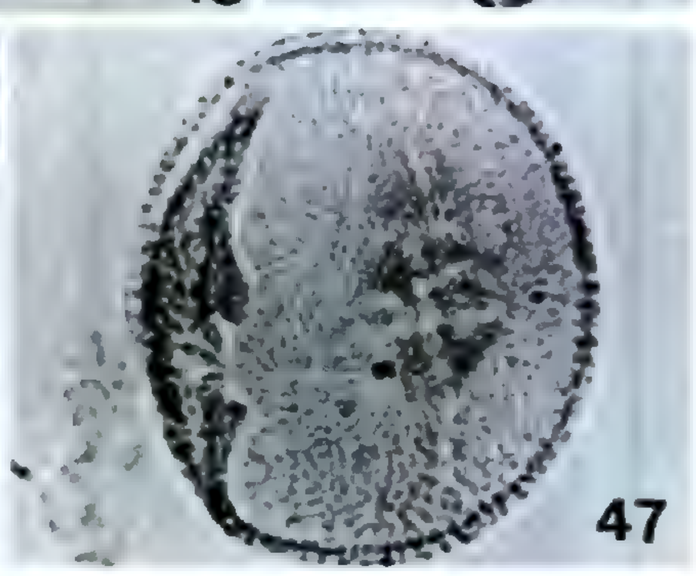

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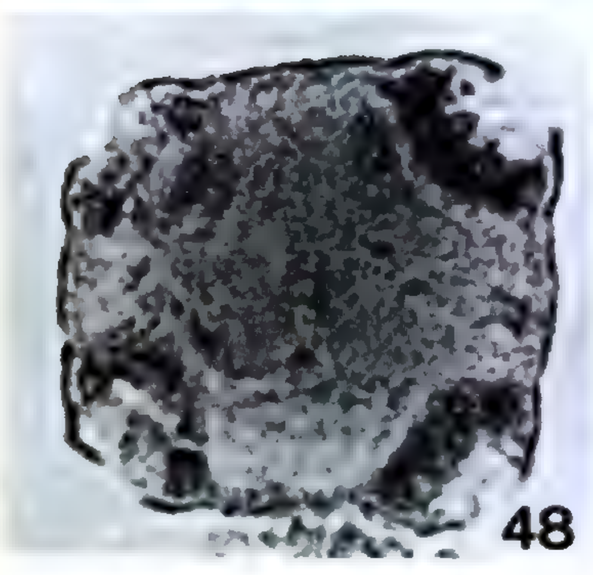

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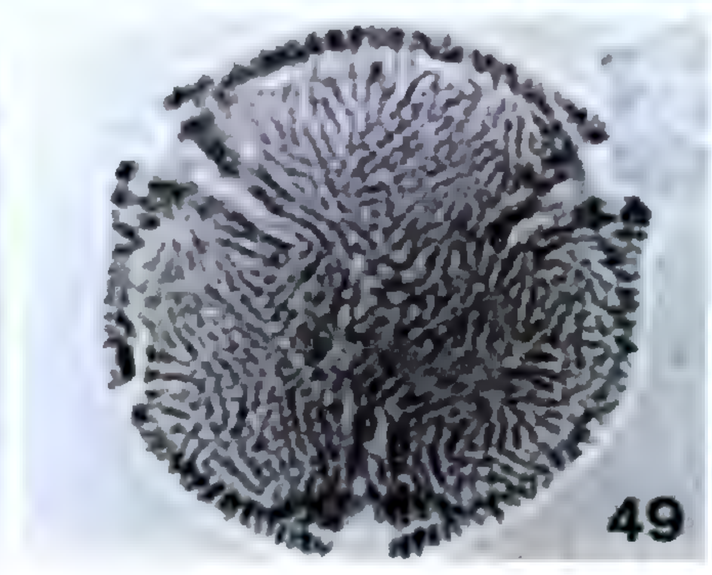

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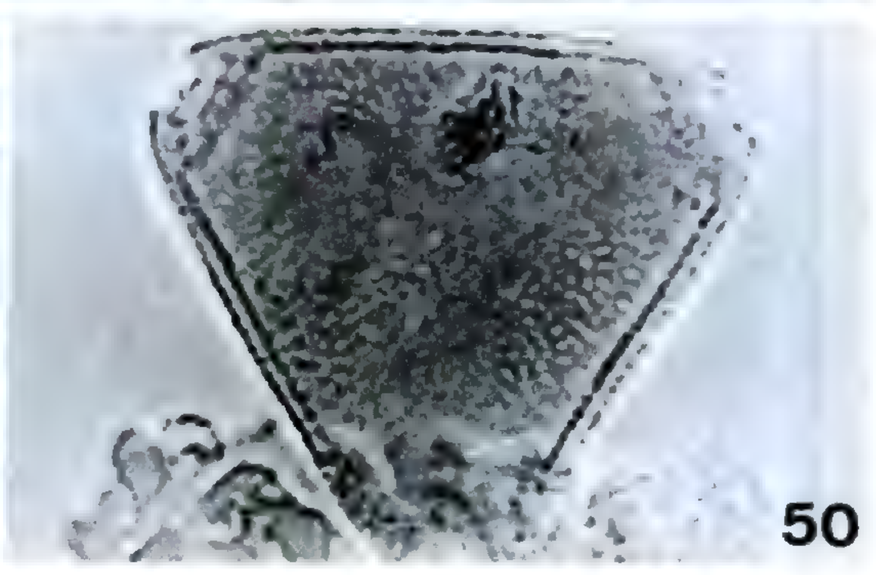

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Guarea (Figs. 39, 42). Oblate-spheroidal, amb circular, tetracolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, relatively short (12–14 μm), faint costae colpi 4–5 μm wide, inner colpus margin entire to minutely dentate, pores conspicuous relative to colpi, situated at midpoint of colpus, circular to slightly elongated equatorially, 6 μm diam., inner margin entire; psilate to faintly scabrate; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 36 × 39 μm.

Guarea is a large genus of about 150 species listed for the American tropics, with about 10 recorded for Panama that encompass a large number of synonymies (D'Arcy, 1987). Two common species in Panama are *G. glabra* Vahl and *G. multiflora* Adr. Juss., which range from Mexico to South America. In Panama these species occur in tropical wet and tropical moist forests at low to moderate elevations.

Guarea has been reported previously from the San Sebastian and Paraje Solo formations.

MYRTACEAE

Eugenia/Myrcia (Fig. 28). Oblate, amb triangular; tricolporate to tricolporoidate, syncolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 12–15 μm long, inner margin minutely dentate, pore obscure, situated at midpoint of colpus, ca. 1.5 μm diam.; scabrate; tectate, wall 2 μm thick, homogeneous (400× magnification); 24–28 μm.

The pollen of these genera cannot be distinguished consistently (Graham, 1980), and it is not possible to identify dispersed fossil pollen below the rank of family. The genera are widespread in Latin America and range through a variety of habitats. Similar pollen has been recovered from the Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, and Paraje Solo formations.

NYMPHAEACEAE (CABOMBACEAE)

Cabomba (Fig. 38). Reniform; monosulcate, sulcus 45 μm long, bordered by faint, narrow (ca. 2 μm) margo; striate, striae appearing finely beaded due to underlying columellae; tectate, wall 2 μm thick, homogeneous (400× magnification); 58 × 34 μm.

Cabomba comprises six species of aquatic herbs in warm temperate to tropical regions of the New World. In Panama it is represented by *G. piauhyensis* Gardner, which has pollen similar to the Gatun specimen. Megafossils are known from the Paleocene Ft. Union Formation of North Dakota (see listings in LaMotte, 1952: 89). Microfossils are known presently only from the Gatun Formation.

ONAGRACEAE

Hauya (Fig. 37). Oblate, amb oval-triangular (aspidate); triporate, pores equatorially arranged, equidistant, large (10–12 μm diam.), slightly protruding, surrounded by conspicuous costae pori, elements of costae pori granular to elongated (striate), oriented parallel to equator; psilate to faintly scabrate; tectate, wall 3–4 μm thick, homogeneous (400× magnification); 102 μm.

Hauya comprises two species in Mexico and Central America: *H. heydeana* J. D. Smith (Chiapas, Mexico, and Guatemala) and *H. elegans* DC. (Hidalgo and Guerrero, Mexico to Costa Rica). It grows "with oaks and other lush middle elevation vegetation. It does not range upward into the pine belt or downward into the seasonally drier deciduous vegetation" (Graham & Jarzen, 1969, from Raven, pers. comm.). *Hauya* has been reported previously from the San Sebastian Formation.

RHIZOPHORACEAE

Rhizophora (Fig. 29). Prolate to prolate-spheroidal; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 12–15 μm long, inner margin entire, costae colpi 2–3 μm wide, pores situated at midpoint of colpus, elongated equatorially (costae transversalis), 1 × 4 μm; finely reticulate; tectate-perforate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 18–20 × 22–24 μm.

Rhizophora is not abundant in the Gatun samples. In the absence of other mangrove genera (e.g., *Pelliciera*), together with the diversity of upland and freshwater types, this suggests deposition in a swamp, shallow lake, or marsh only occasionally influenced by marine or brackish waters. Its geologic record in the Gulf/Caribbean region was summarized by Graham (1989). It is known from all our Tertiary formations in northern Latin America (Gatuncillo, San Sebastian, Uscari, Culebra, Cucaracha, Culebra, La Boca, and Paraje Solo).

RUBIACEAE

Chomelia type (Fig. 40). Spherical, amb circular; nonaperturate (apertures obscure?); coarsely reticulate, muri 2 μm wide, straight, lumina

polygonal, 2–8 μm diam.; tectate-perforate, wall 4–5 μm thick, individual columellae evident in median section (400× magnification); 28–34 μm.

This pollen type is common to several genera of the Rubiaceae (e.g., *Chomelia*, *Guettarda*, *Terebraria*) but is most similar to *Chomelia* in our reference collection. Nine species are listed for Panama (Dwyer, 1980; eleven in D'Arcy, 1987). The Panama species are trees, shrubs, or scandent shrubs growing in a variety of habitats, including swamp forests, tropical moist, and secondary forests. Similar pollen has been recovered from the Culebra, La Boca, and Paraje Solo formations [as the smaller *Terebraria* (22 μm); Graham, 1976, figs. 187–188].

Cosmibuena (Fig. 43). Oblate, amb circular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, oriented parallel to the equator (as observed in polar view), equidistant, 12 μm long, inner margin entire, pore situated at midpoint of colpus, circular, 3–4 μm diam., bordered by beaded annulus of fine, discontinuous ektexine elements; psilate; tectate, wall 2 μm thick, homogeneous (400× magnification); 28 μm.

The genus comprises about 12 species in Central and tropical South America, with two occurring in Panama: *C. ovalis* Standley, and *C. skinneri* (Oersted) Hemsley. The latter is most widespread, distributed from Mexico to Colombia and possibly Brazil. It is a component of tropical moist, premontane wet, and premontane rainforests. *Cosmibuena* is known only from the Gatun Formation.

Faramea type 1 (Fig. 41). Oblate, amb oval-triangular; triporate, pores equatorially arranged, equidistant, slightly protruding, 3–4 μm diam., annulus 3–4 μm wide, faint costae pori(?); finely reticulate, muri ca. 1 μm wide, lumina 1 μm or less in diameter; tectate-perforate, wall 4–5 μm thick; individual columellae evident in median section (400× magnification); 34–39 μm.

Faramea type 2 (Figs. 44, 45, 48). Oblate, amb oval-triangular; triporate, occasionally diporate or tetraporate, pores equatorially arranged, equidistant, circular to slightly oval, ca. 4 μm diam., inner margin entire to slightly dentate, surrounded by conspicuous annulus 5–6 μm wide; scabrate; tectate, wall 1.5 μm thick, wall homogeneous to individual columellae just visible in median section (400× magnification); 27–36 μm.

The pollen of *Faramea* is diverse, including diporate (e.g., Graham, 1985, figs. 64, 65) and tetraporate forms (Fig. 48), and is somewhat polymorphic with both thick-walled and thin-walled forms occurring on the same modern reference slide. Type 1 is similar to *F. talamancarum* Standley in our reference collection, and type 2 is similar to *F. occidentalis* (L.) A. Rich. *Faramea* is a large genus of about 125 species widespread in Latin America (Dwyer, 1980). Nineteen species are listed for Panama (D'Arcy, 1987), and these grow in a variety of habitats, including tropical wet, tropical moist, premontane wet, and premontane moist forests. Various pollen forms of *Faramea* have been recovered from the Gatuncillo, San Sebastian, and Paraje Solo formations.

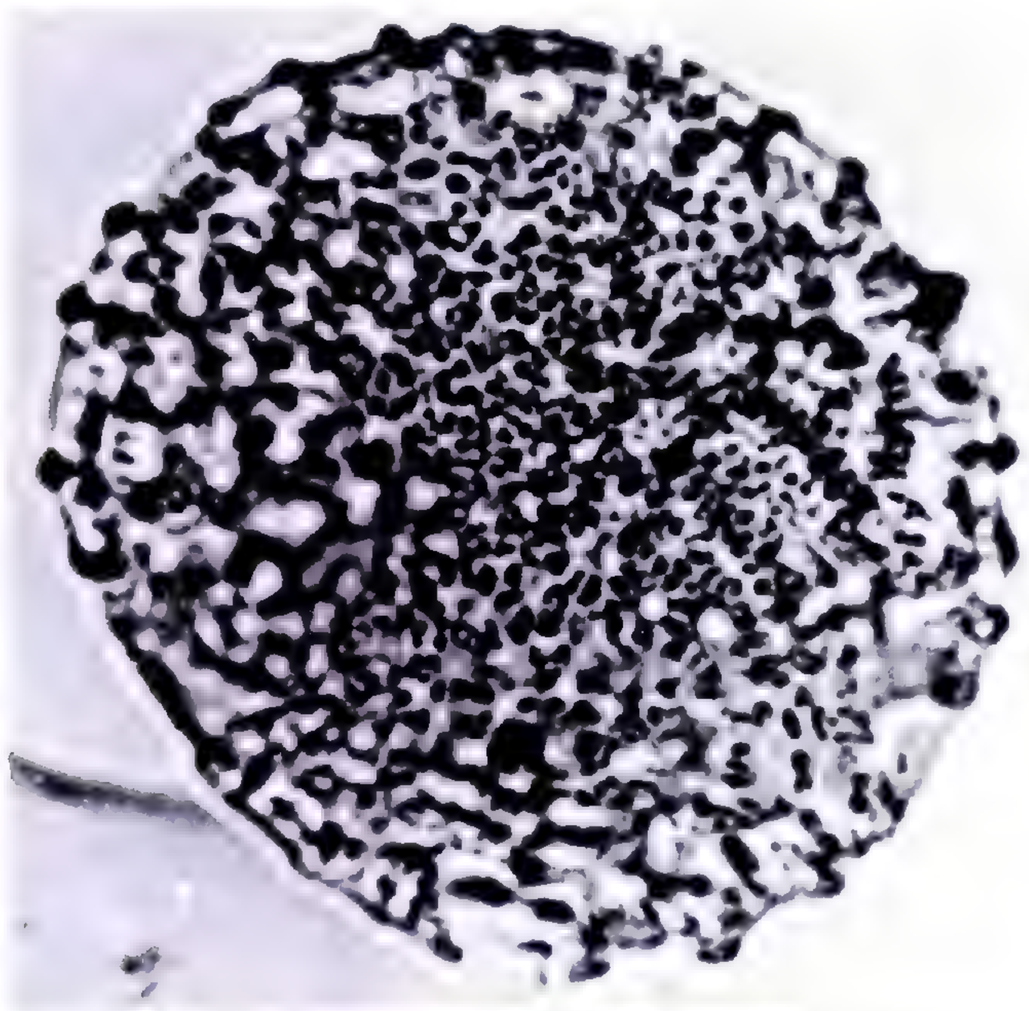
Posoqueria (Figs. 51–53). Spherical to oblate-spheroidal, amb circular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, short (12 μm apex to equator), broad at midpoint (9–12 μm), colpi faint and frequently obscure, pore circular, conspicuous (7–9 μm diam.), situated at midpoint of colpus, bordered by conspicuous annulus 4–5 μm wide; reticulate, reticulum irregular, lumen circular, 6–8 μm diam. in equatorial region, becoming finer and disrupted at poles, columellae supporting reticulum long (3–4 μm) clavae with smaller clavae-baculae occupying lumina of reticulum, muri smooth, slightly sinuous; tectate-perforate, wall 3–4 μm thick, individual columellae evident in median section (400× magnification); 68–70 μm.

Posoqueria includes about 15 species of trees and shrubs in Mexico, South America, and the Antilles. The most widespread species is *P. latifolia* (Rudge) Rose & Standley, growing primarily in the tropical moist forest, but also in tropical wet, premontane wet, premontane moist, and tropical dry forests. *Posoqueria* is known only from the Gatun assemblage.

RUTACEAE

Casimiroa (Figs. 46, 47, 49). Prolate-spheroidal, amb circular; tricolporate, equatorially arranged, colpi meridionally elongated, equidistant, 30 μm long, colpus margin entire to faintly dentate, costae colpi ca. 4–5 μm wide, pore situated at midpoint of colpus, equatorially elongated, 2 × 3 μm, bordered by costae pori 2 μm wide; finely striate-reticulate, arranged in swirl pattern, striae/muri occasionally appearing minutely beaded due to underlying columellae; tectate-perforate, wall 2 μm thick, columellae evident in median section; (400× magnification); 45–40 × 35–40 μm.

Six species of *Casimiroa* occur in Mexico and Central America, but none are listed for Panama (D'Arcy, 1987). Microfossils are known presently only from the Gatun Formation.



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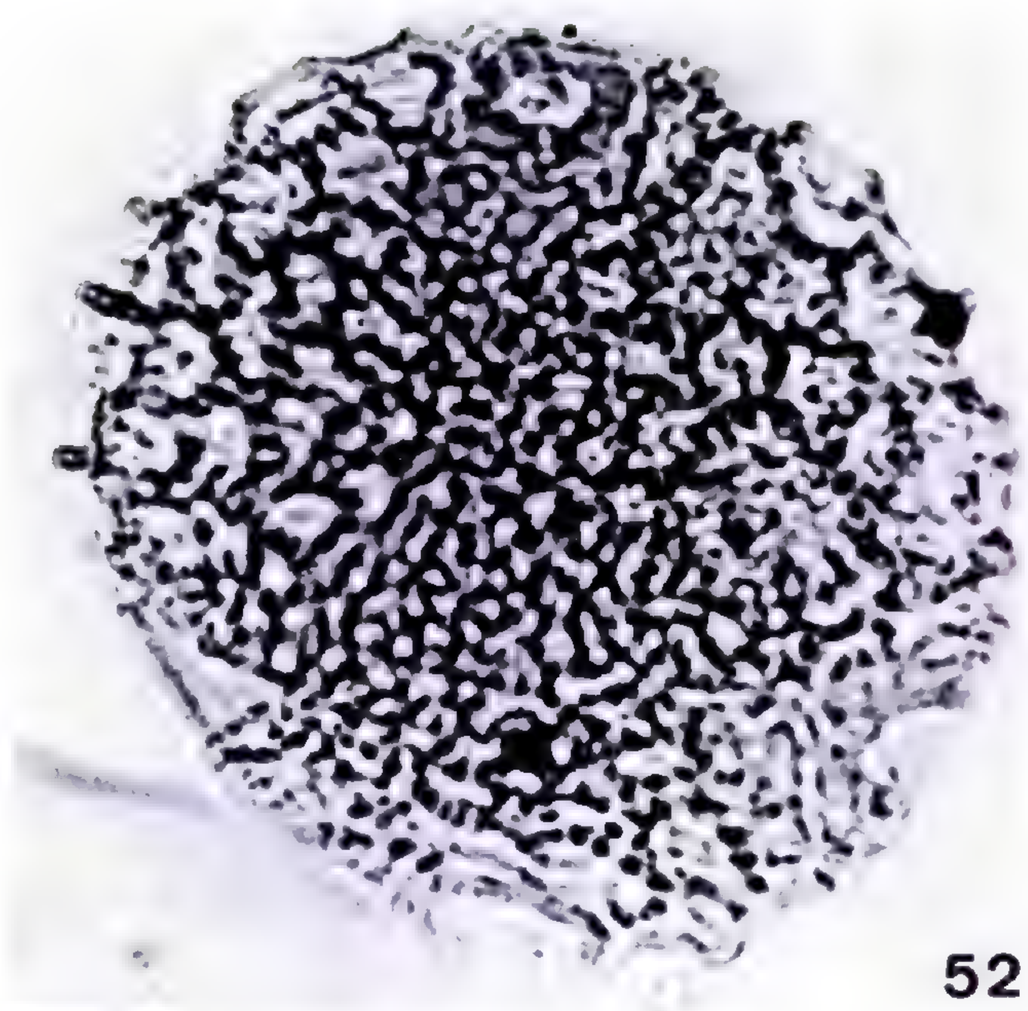

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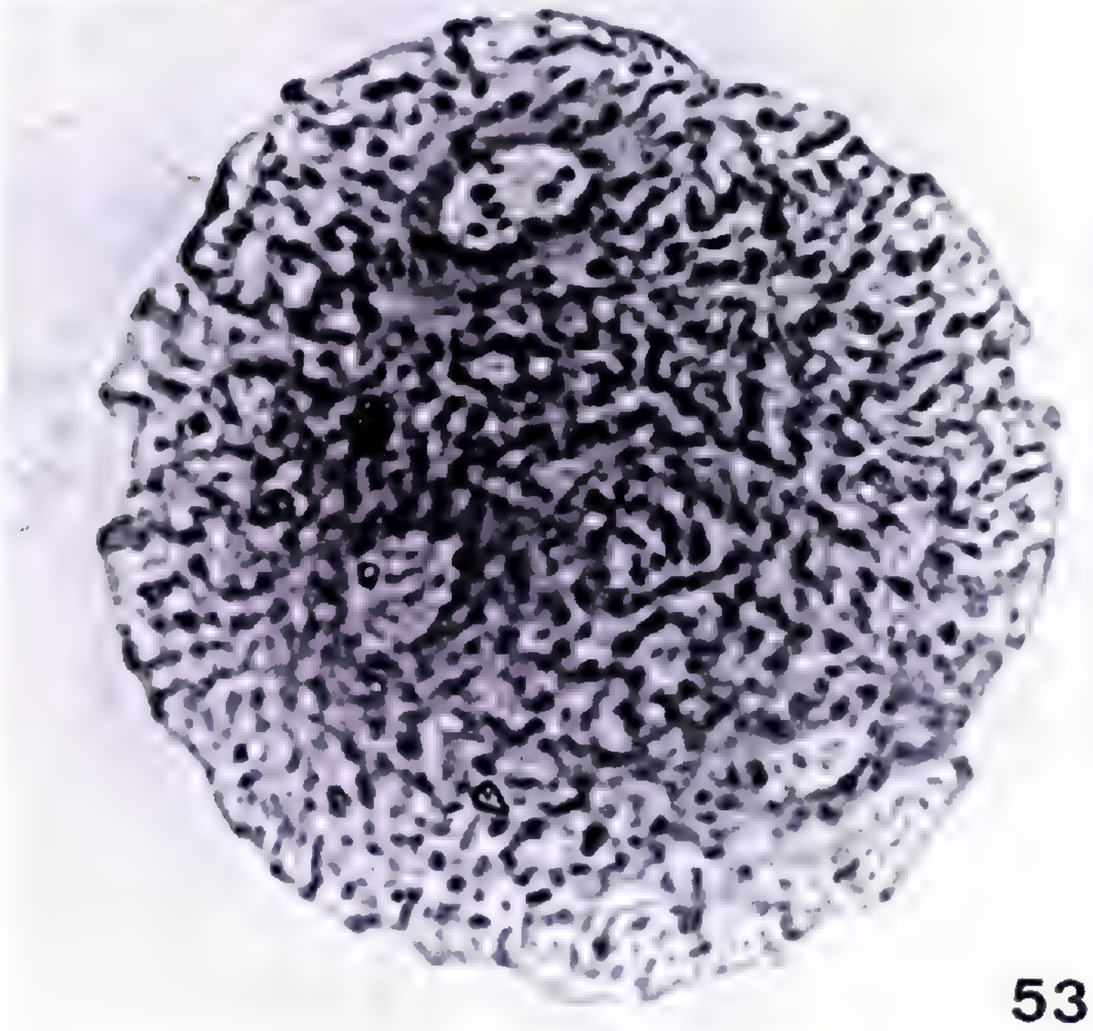

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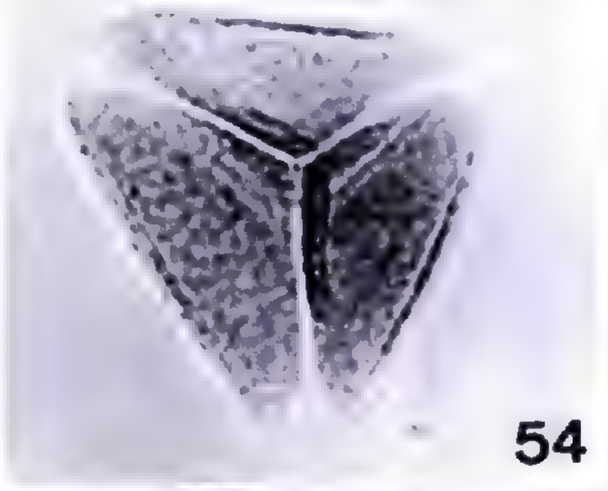

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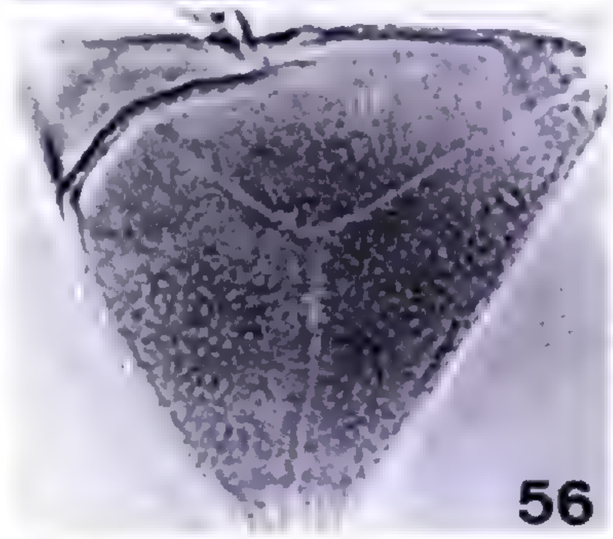

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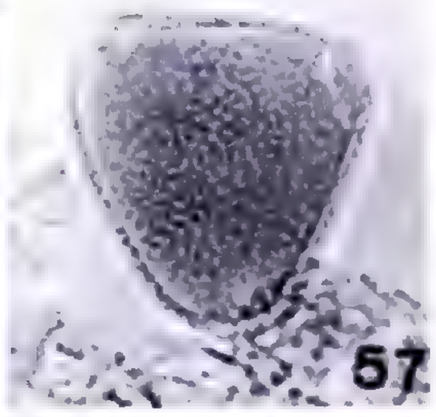

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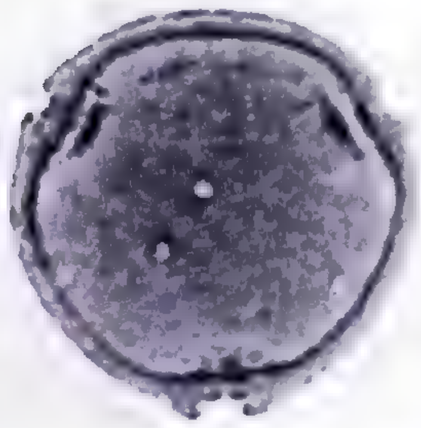

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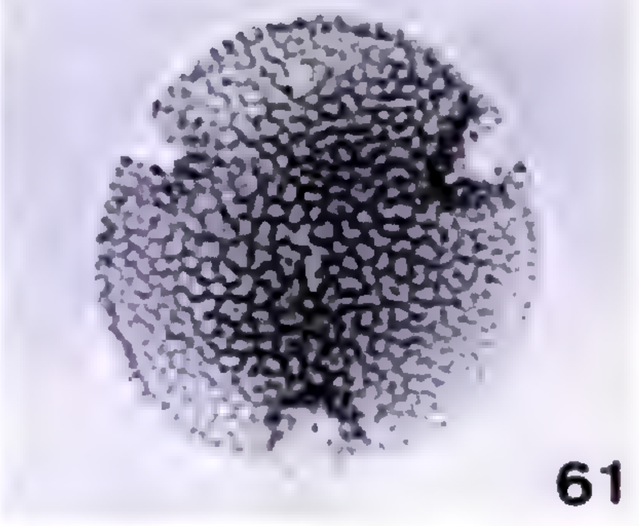

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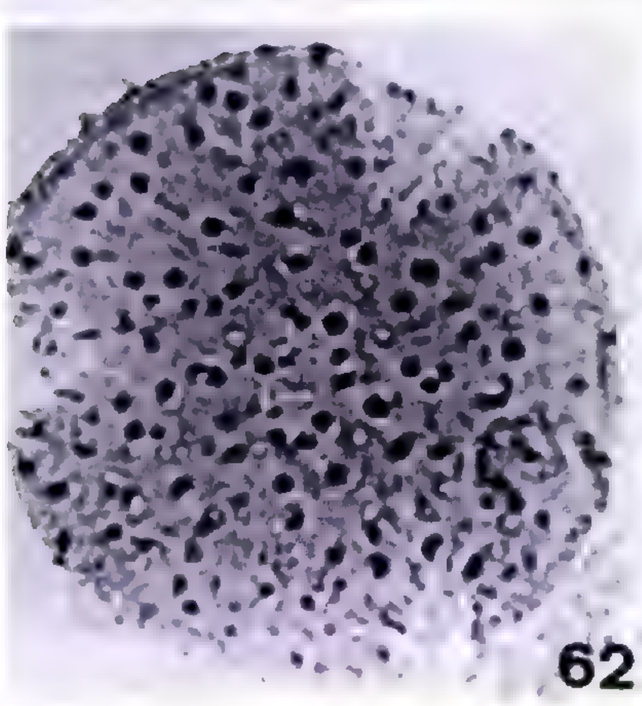

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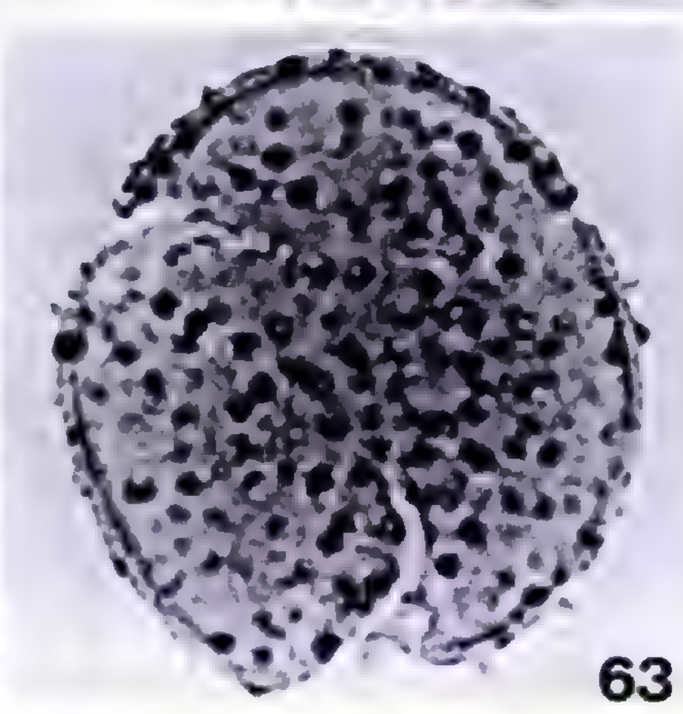

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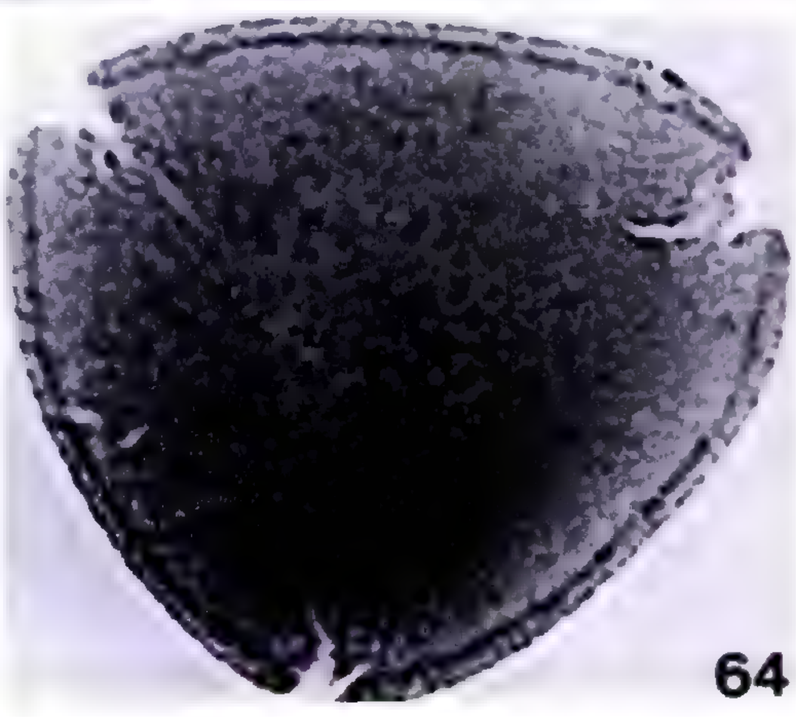

64

SAPINDACEAE

Allophylus (Fig. 57). Oblate to peroblate, amb triangular; triporate, pores equatorially arranged, equidistant, slightly elongated equatorially, 4 × 2 μm, faint costae pori; finely reticulate; tectate-perforate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 21–24 μm.

Allophylus is a large genus of about 190 species, with 13 listed for Panama (D'Arcy, 1987). The plants grow at low to moderate elevations in tropical wet, tropical moist, tropical dry, premontane wet, and premontane moist forests. Similar pollen has been reported from the Culebra and Paraje Solo formations.

Cupania (Figs. 54, 55). Oblate to peroblate, triangular; tricolporoidate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 10–12 μm long, syncolpate, apices of colpi occasionally branched to include triangular polar area; scabrate; tectate, wall 2–3 μm thick, homogeneous (400× magnification); 26 μm.

The pollen of *Cupania* is difficult to distinguish from *Matayba*. Those grains with a moderately thick wall, often including a triangular polar area, are most similar to *C. latifolia* HBK in our reference collection. Eleven species are listed for Panama (D'Arcy, 1987), and these grow primarily in tropical wet, tropical moist, and premontane moist forests. Similar grains are known from the Culebra and Paraje Solo formations.

Paullinia (Fig. 50). Oblate to peroblate, amb triangular; triporate, pores equatorially arranged, equidistant, 4–6 μm diam., costae pori ca. 4 μm wide; finely reticulate; tectate-perforate, wall 2–3 μm thick, individual columellae just visible in median section (400× magnification); 34–38 μm.

Paullinia is a large genus of about 194 neotropical species, with 49 species listed for Panama (D'Arcy, 1987). The plants typically grow in moist forests at low to moderate elevations. Similar pollen has been reported from the Gatuncillo and Paraje Solo formations.

Serjania (Fig. 56). Oblate to peroblate, amb triangular; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 22–25 μm long, inner margin entire, syncolpate, pores situated at midpoint of colpus, 3–4 μm diam., faint costae pori; finely reticulate; tectate-perforate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 36–40 μm.

Twenty species of *Serjania* are recorded for Panama (D'Arcy, 1987), and these occur through a wide range of habitats at low to moderate elevations. Similar pollen has been reported from the Gatuncillo and Paraje Solo formations.

SAPOTACEAE

cf. Bumelia (Fig. 58). Prolate; tetracolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 18–21 μm long, inner margin entire to minutely dentate, costae colpi ca. 3 μm wide, pores situated at midpoint of colpus, elongated equatorially (colpi equatorialis), 2–3 × 4–5 μm, inner pore margin entire; psilate; tectate, wall 3 μm thick, homogeneous (400× magnification); 32–35 × 23–26 μm.

Pollen of tetra-aperturate Flacourtiaceae, Meliaceae, and Sapotaceae is difficult to distinguish consistently, especially in the dispersed fossil state. The Gatun specimens are most similar to *Bumelia* in our reference collection. *Bumelia* is a New World genus of about 23 species of trees and shrubs, ranging from the United States to Mexico, South America, and the Antilles (Blackwell, 1968). A single species, *B. persimilis* Hemsley, is listed for Panama (D'Arcy, 1987) and is distributed from Veracruz and Oaxaca, Mexico, to Venezuela. This pollen type was not reported previously in our Gulf/Caribbean assemblages.

SYMPLOCACEAE

Symplocos type 1 (Fig. 59). Oblate, amb oval-triangular to nearly circular; triporate (or tricolporate but with colpi short and obscure), pores equatorially arranged, equidistant, circular, 3 μm diam., annulus 3 μm wide; psilate to faintly sca-

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FIGURES 51–64. Fossil pollen from the Gatun Formation.—51–53. *Posqueria*, SL-103, 253′, 4, ESF P-19; SL-103, 253′, 8, ESF U-27.—54, 55. *Cupania*, SL-103, 253′, 8, ESF P-44; SL-103, 253′, 13, ESF J-42.—56. *Serjania*, SL-103, 253′, 15, ESF S-49.—57. *Allophylus*, SL-103, 253′, 2, ESF H-50.—58. cf. *Bumelia*, SL-103, 253′, 12, ESF T-47.—59. *Symplocos* type 1, SL-103, 178′, 2, ESF E-35.—60. *Symplocos* type 2, SL-103, 253′, 5, ESF V-33.—61. *Mortoniodendron*, SL-103, 253′, 13, ESF W-23.—62, 63. *Aegiphila*, SL-103, 253′, 12, ESF J-26; SL-103, 253′, 9, ESF T-48.—64. *Petrea*, SL-103, 255.5′, 5, ESF S-34.

brate; tectate, wall 3 μm thick, homogeneous (400× magnification); 28 μm.

Symplocos type 2 (Fig. 60). This specimen is similar to type 1 but is larger (38 μm). Type 1 is comparable to *S. chiriquensis* Pittier, and type 2 to *S. pychantha* Hemsley, in our reference collection.

Symplocos comprises about 350 species of trees and shrubs of pantropical distribution growing in a wide variety of habitats. Megafossils have been reported from the late Eocene Goshen Formation of Oregon (Chaney & Sanborn, 1933), and microfossils from the Maastrichtian of California (Chumura, 1973). It is known only from the Gatun Formation in the Tertiary of northern Latin America.

TILIACEAE

Mortoniodendron (Fig. 61). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (6–7 μm apex to equator), inner margin minutely dentate, costae colpi 4–5 μm wide; finely reticulate; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 34–38 μm.

The pollen of *Mortoniodendron* and its fossil record has been summarized by Graham (1979). The genus comprises about five species of small shrubs to tall trees growing from southern Mexico through Central America in tall moist forests at low to moderate elevations. Similar pollen has been recovered from the Gatuncillo and Paraje Solo formations.

VERBENACEAE

Aegiphila (Figs. 62, 63). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (9–12 μm apex to equator), inner colpus margin entire to slightly diffuse; echinate, echinae short (ca. 1 μm), moderately dense and uniformly distributed; tectate, wall ca. 1.5 μm thick, individual columellae just visible in median section (400× magnification); 45 μm.

Aegiphila comprises about 160 species of trees, shrubs, and lianas distributed from Mexico to South America (Brazil, Colombia, Venezuela, the Guianas, Peru). Twenty-one species are presently listed for Panama (D'Arcy, 1987), primarily in tropical wet, tropical moist, premontane wet, and premontane moist forests. The Gatun specimens are similar to *A. elata* Sw., a widespread species found along the margins of woods and streams. Fossil pollen of *Aegiphila* is known only from the Gatun Formation.

Petrea (Fig. 64). Oblate, amb oval-triangular, tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (6–8 μm apex to equator), margin entire to minutely dentate; scabrate; tectate, wall 3 μm thick, individual columellae just visible in median section (400× magnification); 52–56 μm.

There are about 30 species of *Petrea* distributed from northern Mexico to southern Brazil and the Antilles. Four species are known from Panama (D'Arcy, 1987), including the widespread *P. aspera* Turcz., which produces pollen similar to the specimens. Megafossils identified as *Petrea* have been reported from the late Eocene (now dated as earliest Oligocene) La Porte flora of California (Potbury, 1935). However, the holotype has an inflated, possibly cross-striated petiolule, which indicates that it is a legume (Doyle et al., 1988). Microfossils are known presently only from the Gatun assemblage.

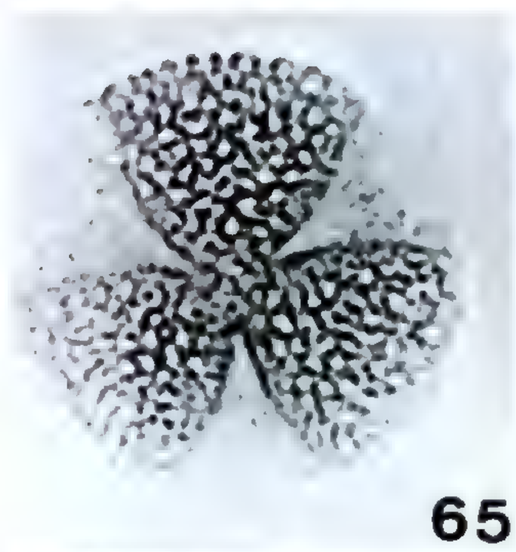
UNKNOWNS

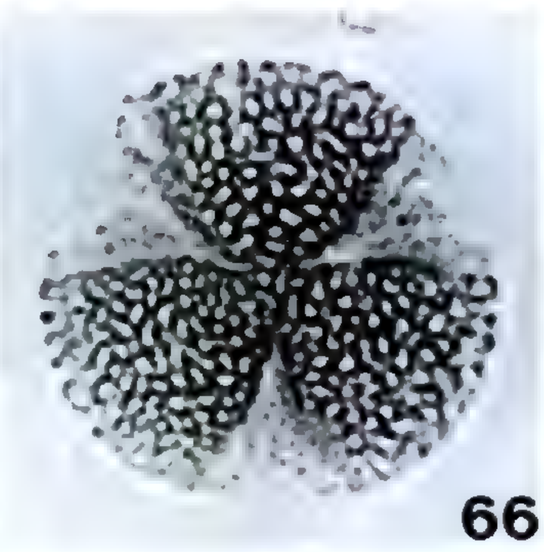
In addition to the specimens identified from the Gatun Formation, a number of unknowns were recovered. Twenty-seven of the more common and/or distinctive ones are described below.

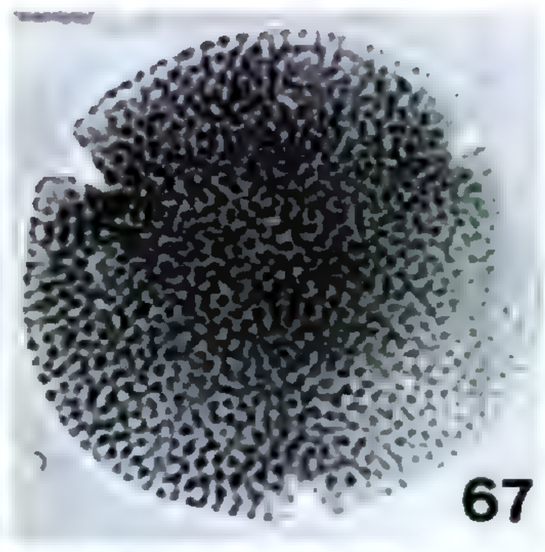
Unknown 1 (Figs. 65, 66). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 16–18 μm long (apex to equator), inner margin finely dentate; finely reticulate, width of muri 1 μm or less, diameter of lumina ca. 1.5 μm; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 35–40 μm.

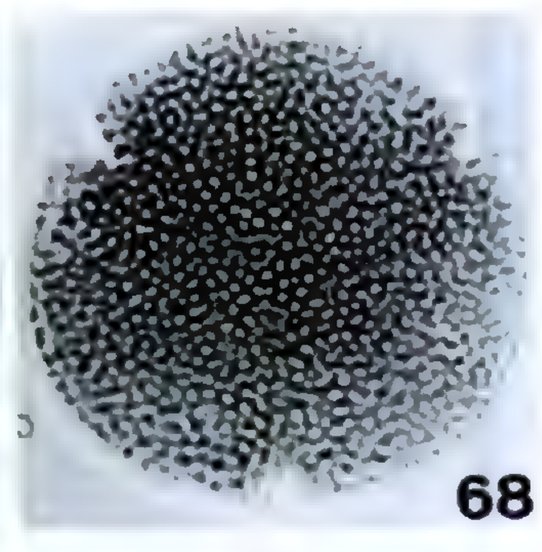
These grains are similar to *Avicennia*, but all are oriented in polar view (*Avicennia* is prolate to prolate-spheroidal and is usually seen in equatorial view), and the wall is slightly thinner in the specimen.

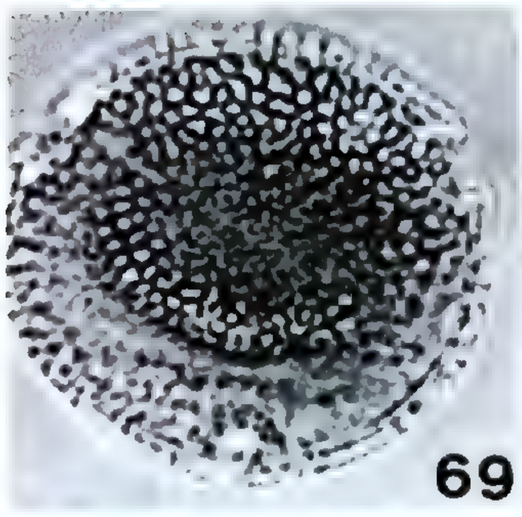
Unknown 2 (Figs. 67, 68). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, short (3–4 μm apex to equator), inner margin finely dentate; finely reticulate, width of muri and diameter of lumina ca. 1 μm; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 35–39 μm.

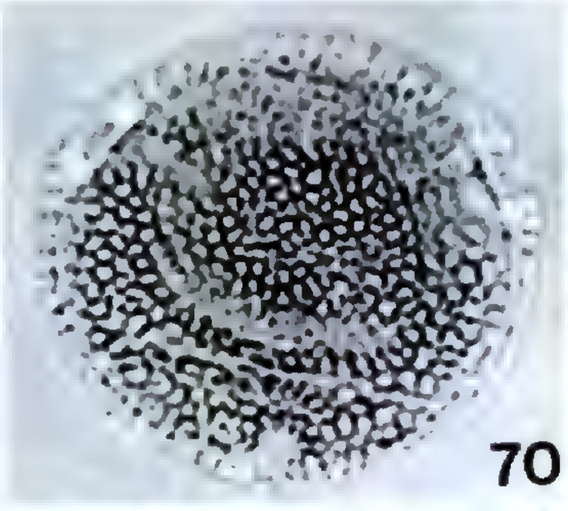


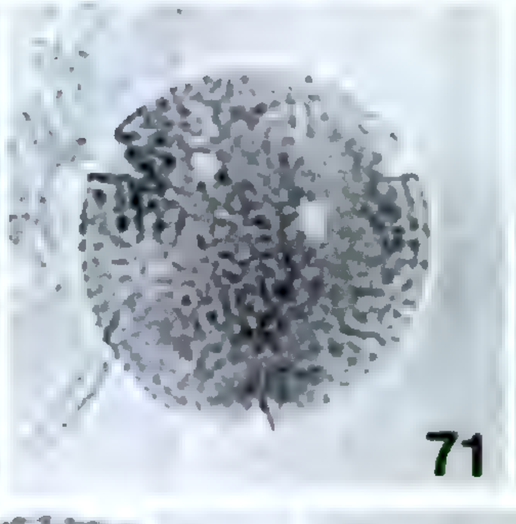


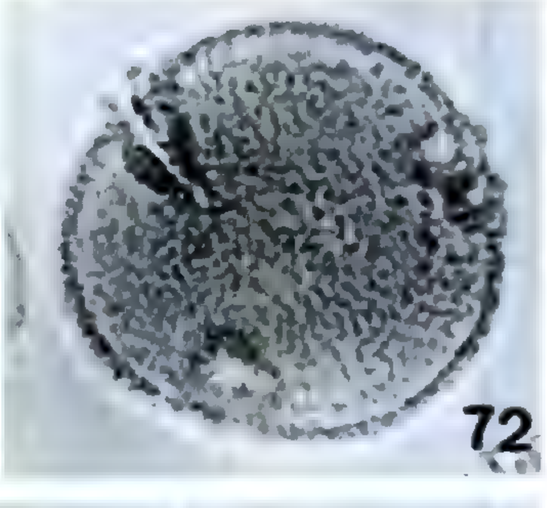


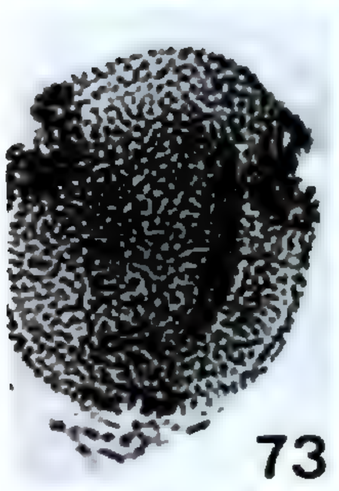


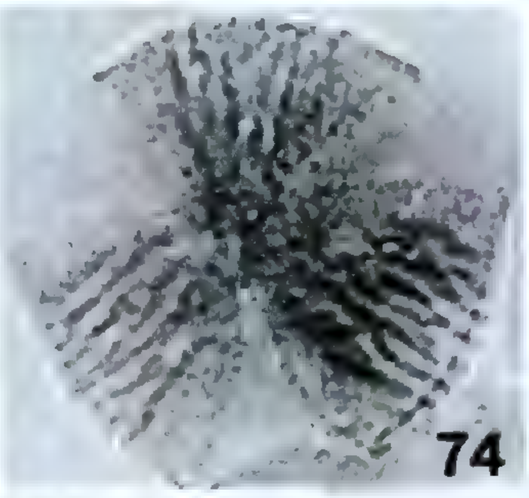


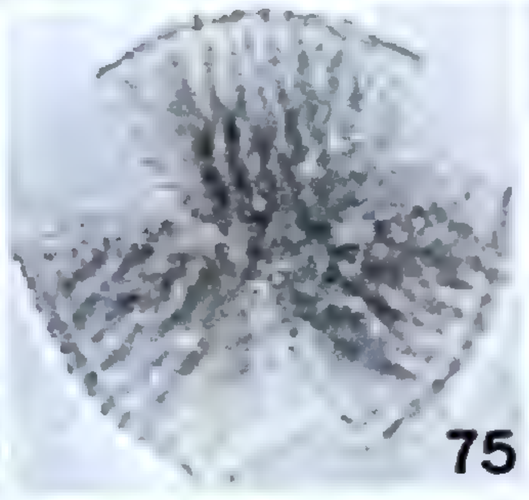


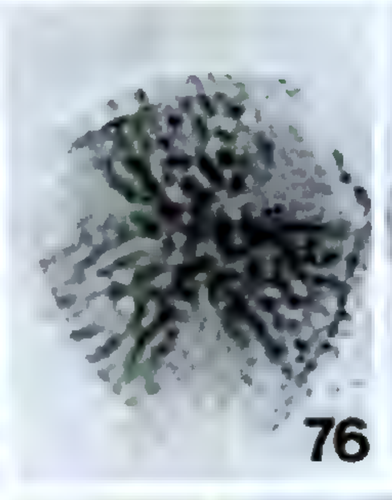


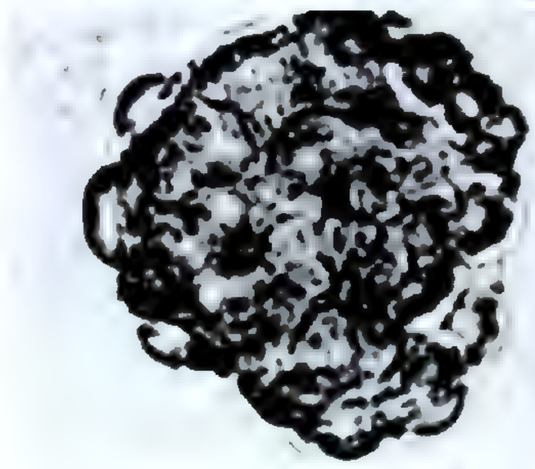


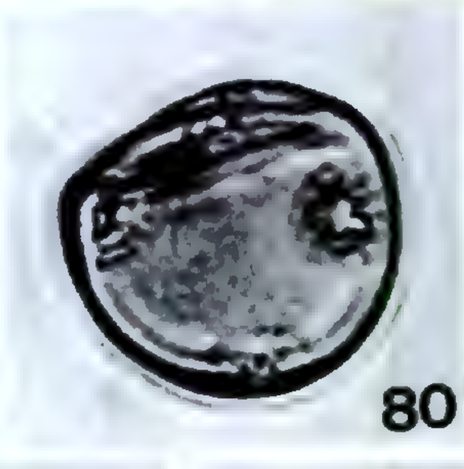


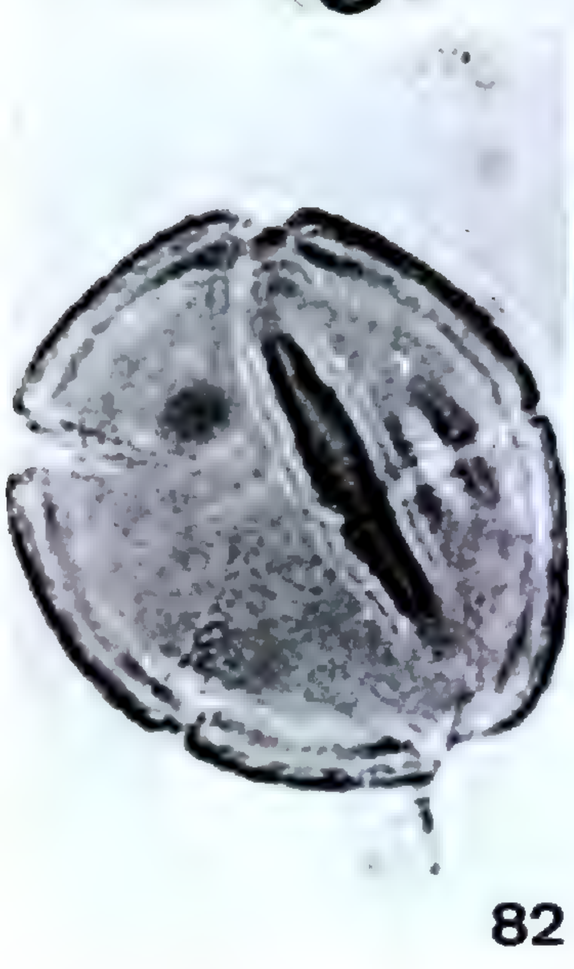


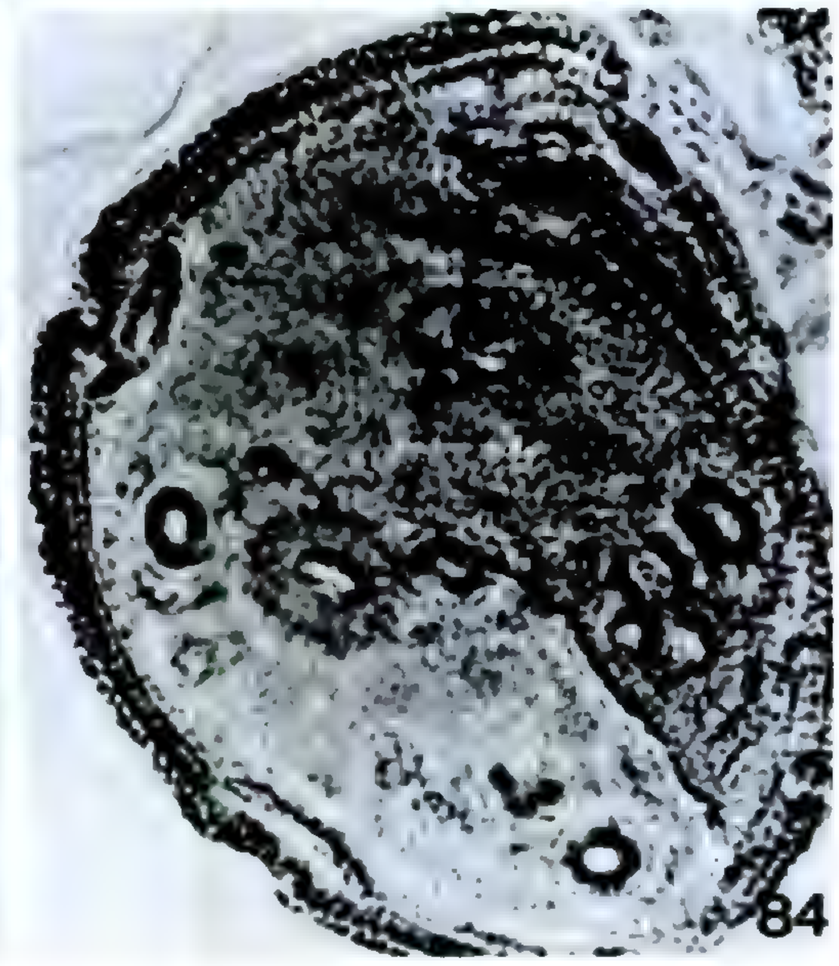












FIGURES 65–84. Fossil pollen from the Gatun Formation.—65, 66. Unknown 1, SL-103, 253′, 1, ESF F-47.—67, 68. Unknown 2, SL-103, 253′, 1, ESF H-52.—69, 70. Unknown 3, SL-103, 253′, 7, ESF W-40.—71. Unknown 4, SL-103, 253′, ESF S-40.—72. Unknown 5, SL-103, 253′, 1, ESF P-37.—73. Unknown 6, SL-103, 257′, 1, ESF P-34.—74–77. Unknown 7, SL-103, 253′, 14, ESF Q-53; SL-103, 253′, 12, ESF M-40.—78. Unknown 8, SL-103, 253′, 15, ESF Q-41.—79, 80. Unknown 9, SL-103, 253′, 10, ESF J-42; SL-103, 253′, 13, ESF N-30.—81. Unknown 10, SL-103, 253′, 7, ESF T-27.—82. Unknown 11, SL-103, 253′, 5, ESF F-19.—83. Unknown 12, SL-103, 253′, 5, ESF O-14.—84. Unknown 13, SL-103, 253′, 7, ESF U-27.

Unknown 3 (Figs. 69, 70). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally arranged, equidistant, short (3 μm apex to equator), inner margin finely dentate; finely reticulate, width of muri and diameter of lumina ca. 1 μm; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 31–34 μm.

The wall of unknown 2 is slightly thinner and the columellae finer than in unknown 3. The short colpi and fine reticulum of these unknowns are suggestive of the Bombacaceae, but no exact match could be found among modern analogs in our reference collection.

Unknown 4 (Fig. 71). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (3–4 μm apex to equator); scabrate; tectate, wall 2 μm thick, columellae just visible in median section (400× magnification); 23–26 μm.

Unknown 5 (Fig. 72). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (6–7 μm apex to equator), costae colpi 3 μm wide; scabrate; tectate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 29–34 μm.

Unknown 6 (Fig. 73). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, short (6–7 μm apex to equator), costae colpi 4–5 μm wide; finely reticulate, width of muri and diameter of lumina ca. 1 μm; tectate-perforate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 32–35 μm.

Unknown 7 (Figs. 74–77). Oblate, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, 12–15 μm long (apex to equator), broad (10–14 μm at equator, possibly compressed open), inner colpus margin diffuse; striate, striae coarse (3 μm wide), slightly sinuous, parallel and oriented at right angle to equatorial plane; tectate, wall 2 μm thick, homogeneous; 22–33 μm.

Unknown 8 (Fig. 78). Oblate-spheroidal, amb circular; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, colpi obscured by sculpture elements; verrucate, verrucae mound-like, translucent, variable in size, larger ca. 6 μm diam., base of verrucae and intervening surface area with small columellae giving granular appearance to portions of grain surface; tectate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 28–32 μm.

These grains are somewhat similar to *Elizabetha* (Leguminosae–Caesalpinioideae), but are smaller and have fine columellae giving a granular appearance to portions of the exine surface. They are also present in the La Boca (Graham, 1989, figs. 55, 56) and Paraje Solo (Graham, 1976, figs. 244, 245) formations.

Unknown 9 (Figs. 79, 80). Oblate-spheroidal to spherical, amb circular; tetraporate, pores equatorially arranged, equidistant, circular, 3 μm diam., annulus 3 μm wide, outer margin of annulus irregular and slightly granular; psilate; tectate, wall 2 μm thick, homogeneous (400× magnification); 22–25 μm.

These grains are very similar to *Cosmibuena* (Fig. 43) and may represent tetraporate forms of that genus. However, tetraporate grains have not been observed in our modern reference material of *Cosmibuena*, hence the designation of these specimens as unknown.

Unknown 10 (Fig. 81). Oblate, amb circular; stephano(5)colporate, colpi equatorially arranged, meridionally elongated, equidistant, short (ca. 5 μm), narrow (1 μm), inner margin minutely dentate, pores situated at midpoint of colpus, equatorially elongated, ca. 2 × 4 μm, costae pori; psilate; tectate, wall 2–3 μm thick, homogeneous (400× magnification); 31–33 μm.

Unknown 11 (Fig. 82). Oblate, amb circular; stephano(5)colporate, colpi equatorially arranged, meridionally elongated, equidistant, 15–18 μm long, tapering to prolonged acute apex, inner margin entire, pores situated at midpoint of colpus, 3 × 9 μm; scabrate to finely verrucate, scabrae/verrucae low, larger ca. 5 μm diam.; tectate, wall 4–5 μm diam., homogeneous (400× magnification); 45 μm.

Unknown 12 (Fig. 83). Oblate, amb triangular, apices rounded; trilete or trichotomosulcate, individual arms straight, ca. 30 μm long, extending to or nearly to margin, inner margin entire; scabrate/punctate, punctae (or spaces between scabrae) narrow, elongated, sinuous, becoming finely reticulate bordering apertures; tectate to tectate-perforate, wall 3 μm thick, individual columellae/punctae evident in median optical section (400× magnification); 60 μm.

This specimen may represent a trilete fern spore, but the wall structure suggests a trichotomosulcate palm pollen.

Unknown 13 (Fig. 84). Spherical, amb circular; periporate, pores circular, 3–4 μm diam., evenly distributed, inner margin entire, costae pori 4–5 μm wide; scabrate; tectate, wall 4 μm thick, individual columellae evident in median section (400× magnification); ca. 75 μm.

Unknown 14 (Fig. 85). Spherical, amb circular; nonaperturate; echinate, echinae short (2–3 μm), somewhat variable in shape, mostly broad at base, moderately densely arranged, distance between echinae 1–3 μm; tectate, wall 2 μm thick, homogeneous (400× magnification); 75–80 μm.

The size and ornamentation of this grain suggest Cucurbitaceae, but an exact match could not be found. Some of the several folds simulate a trilete mark, but the specimen is provisionally interpreted as nonaperturate.

Unknown 15 (Fig. 86). Oblate, amb circular; stephano(6)colpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 20–22 μm long, inner margin minutely dentate; reticulate, muri narrow (1 μm or less), sinuous, lumina polygonal, ca. 3 μm diam., slightly smaller at poles; tectate-perforate, wall 3 μm thick, individual columellae (appearing as slight clavae) evident in median section (400× magnification), ca. 1 μm wide, spaced ca. 2 μm; 70–75 μm.

The specimen is similar to some Labiatae (e.g., *Hyptis*), but an exact match could not be found.

Unknown 16 (Fig. 92). Spherical, amb circular; nonaperturate; echinate, echinae 3–5 μm long, uniform width (2 μm) for most of length, then tapering abruptly near apex, occasionally curved; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 58 μm (excluding spines).

An irregular fissure extending nearly the entire length of the grain may represent a sulcus, but the margins are irregular, suggesting a split in the exine, and the specimen is interpreted provisionally as nonaperturate.

Unknown 17 (Fig. 91). Spherical, amb circular; nonaperturate; echinate, echinae 7–9 μm long, 3 μm wide at base, occasionally curved, more or less widely spaced (distance between echinae 6–10 μm), surface between spines scabrate; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 52 μm (excluding spines).

Unknown 18 (Figs. 87, 88). Oblate, amb circular; nonaperturate; reticulate, reticulum more or less obscure, shallow, muri narrow, sinuous, lumina polygonal; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 60 μm.

Unknown 19 (Figs. 97, 98). Oblate, amb circular; tricolpate (?, apertures obscure), colpi equatorially arranged, meridionally elongated, equidistant; reticulate, reticulum shallow (supporting columellae short, ca. 1.5 μm), muri narrow (1 μm or less), sinuous, lumina polygonal, larger lumina 3–5 μm diam.; tectate-perforate, wall 2 μm thick, individual columellae evident in median section (400× magnification); 65 μm.

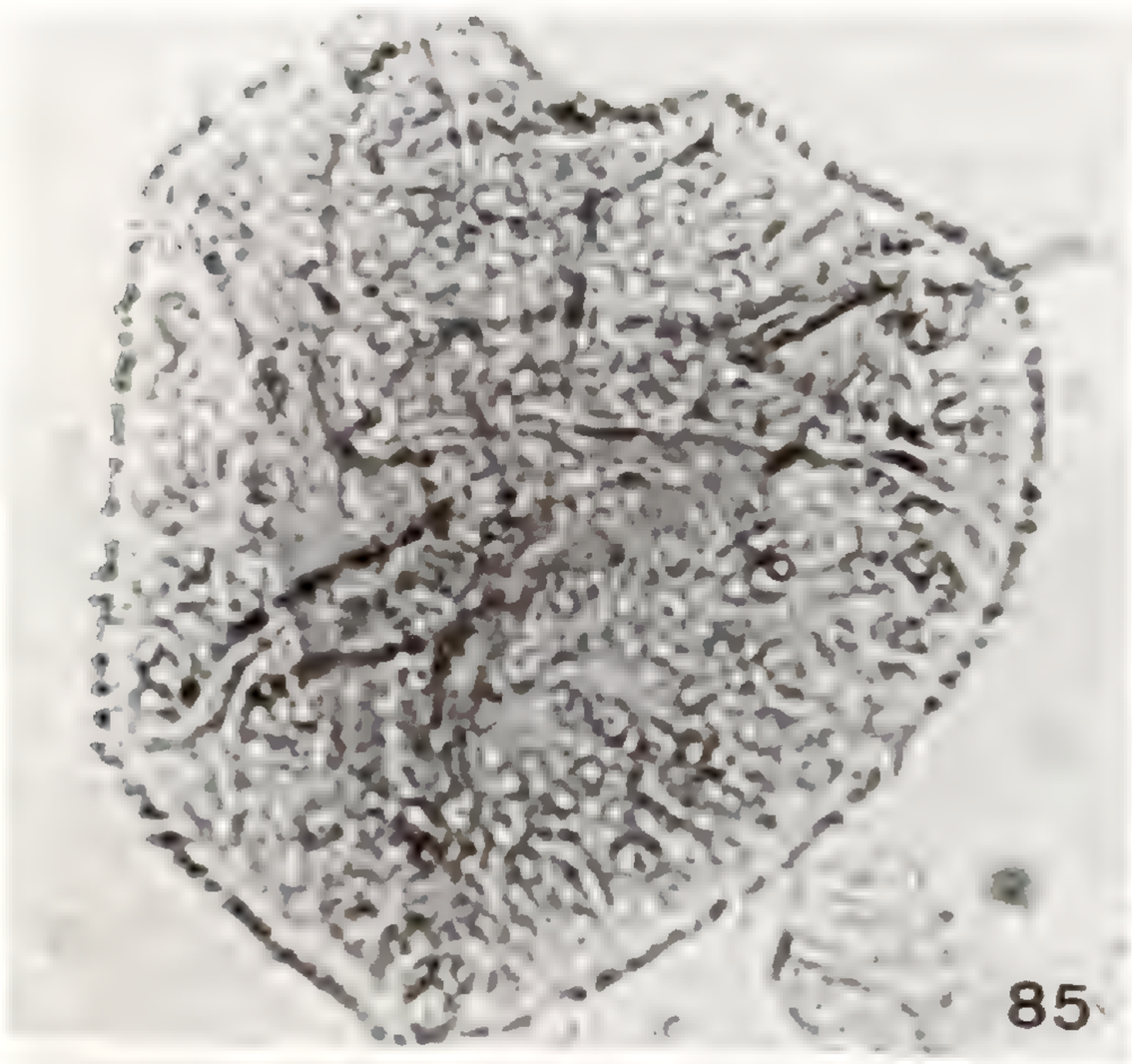
Unknown 20 (Figs. 89, 90). Oblate, amb square; apertures obscure, four(–six) colpi or colpi with pores, apertures equatorially arranged, meridionally elongated, equidistant, with two additional apertures possibly at each pole; finely reticulate, width of muri and diameter of lumina 1 μm or less; tectate-perforate, wall 3 μm, individual columellae evident in median section (400× magnification); 35 μm.

This specimen may be an aberrant form. There appear to be four colpi (with pores?) about the equator, and one at each pole. Grains with a similar number and arrangement of apertures were not encountered in the modern reference collection or in the literature examined.

Unknown 21 (Fig. 95). Prolate to prolate-spheroidal; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, 22–24 μm long, extending nearly entire length of grain, inner margin entire; reticulate, reticulum heavy (columellae ca. 2 μm thick), width of muri and diameter of lumina ca. 1 μm, lumina circular to polygonal; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 28 × 26 μm.

Unknown 22 (Fig. 94). Prolate to prolate-spheroidal; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, colpi straight, narrow, 18–20 μm long, inner margin entire, costae colpi 3–4 μm wide, broadening at pores, pores situated at midpoint of colpus, slitlike (1 × 4–5 μm); psilate to faintly scabrate; tectate, wall 3 μm thick, individual columellae just visible in median section (400× magnification); 27 × 23 μm.

Unknown 23 (Fig. 96). Prolate to prolate-spheroidal, tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, colpi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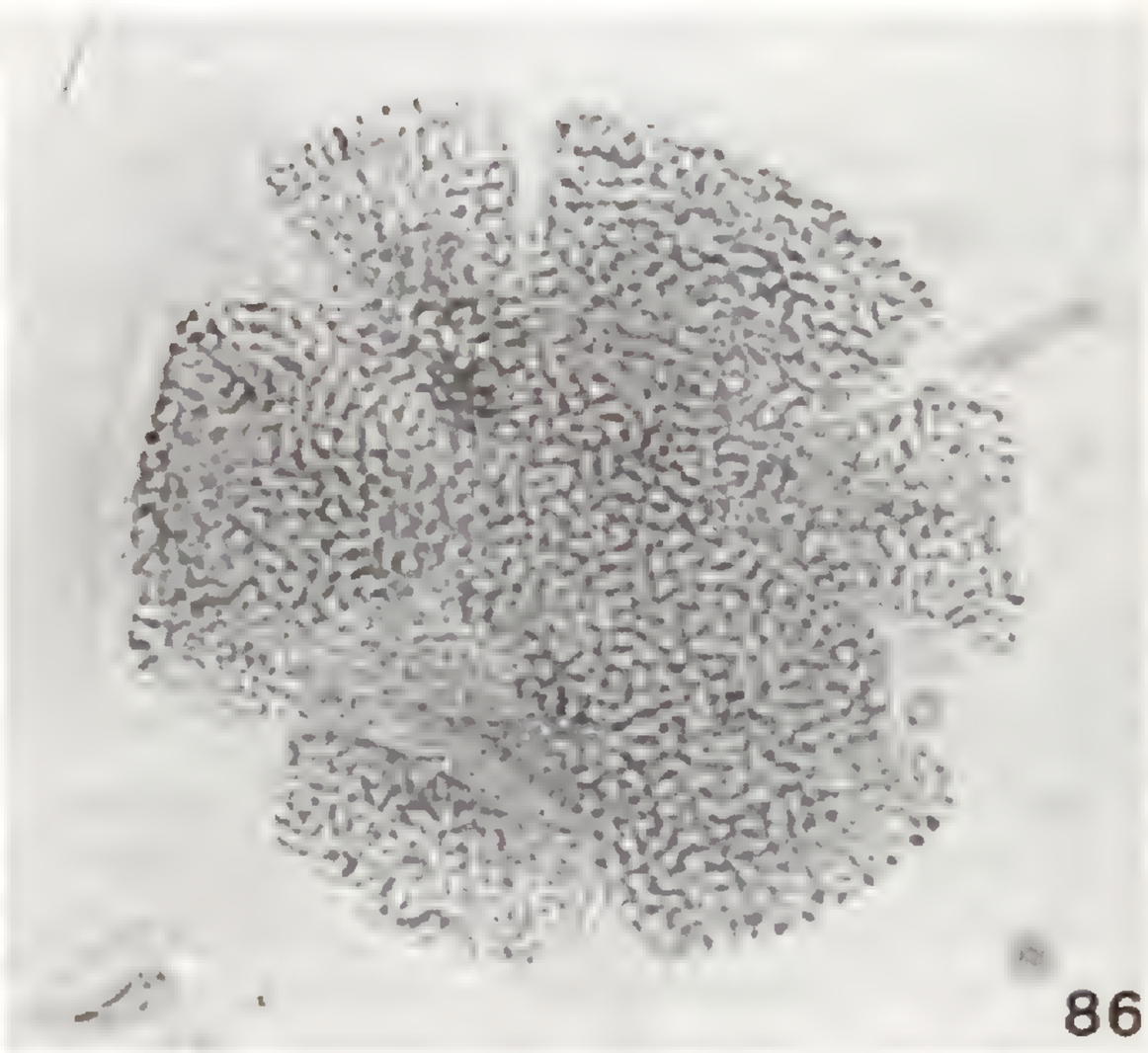
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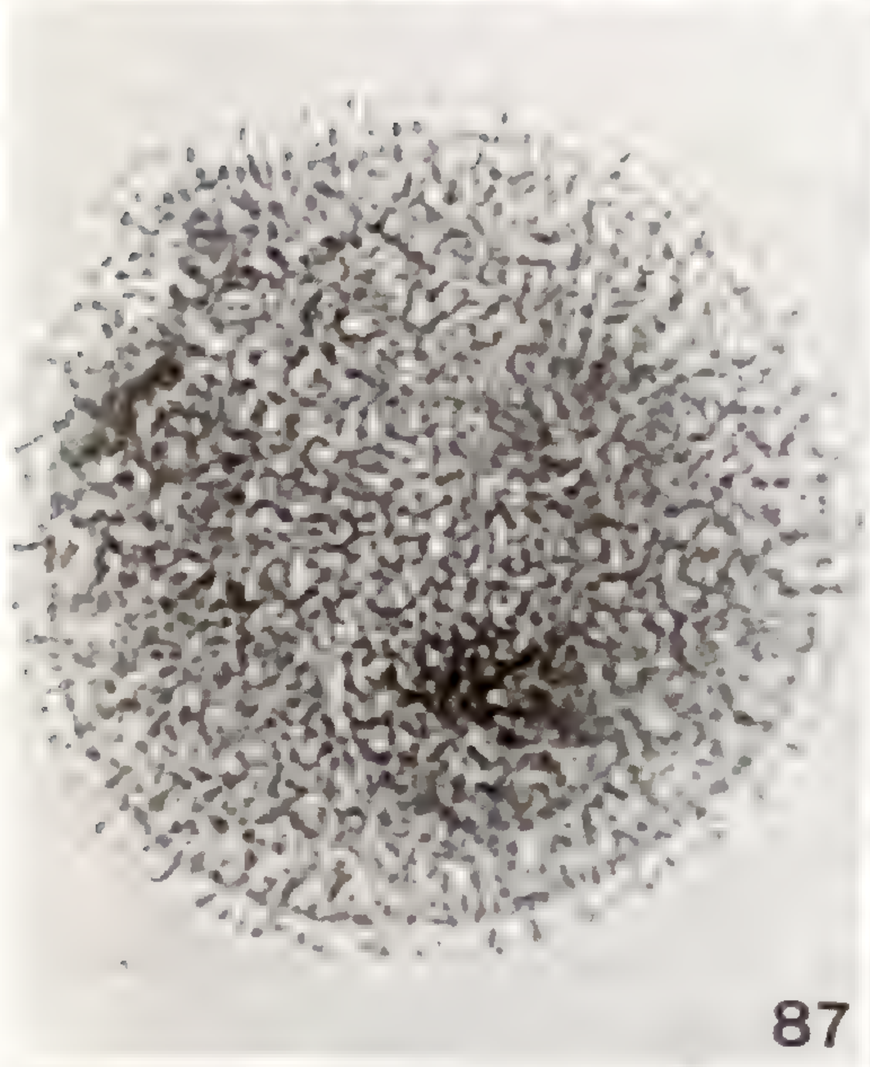
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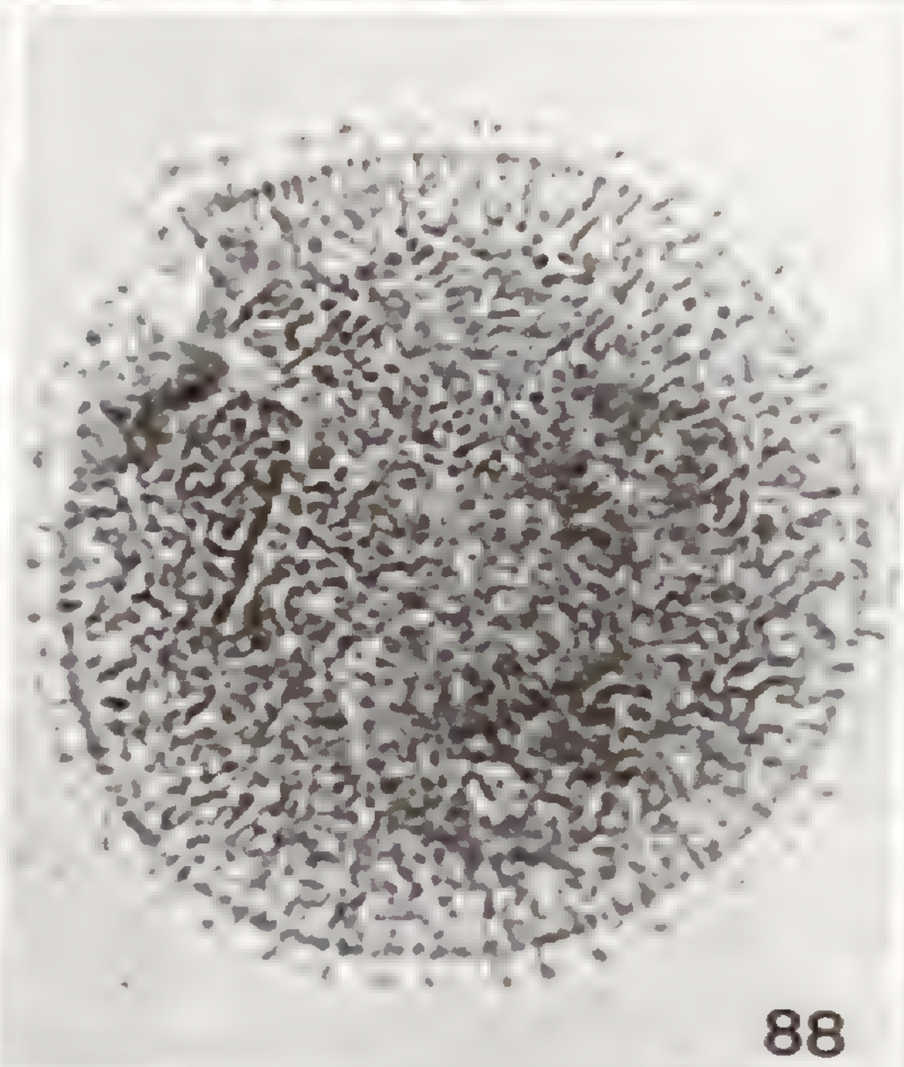
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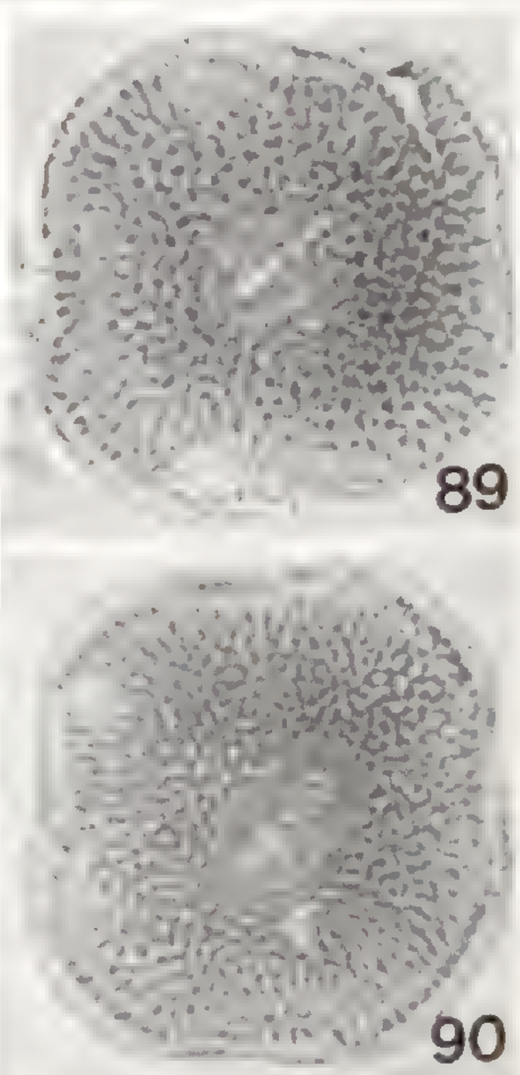
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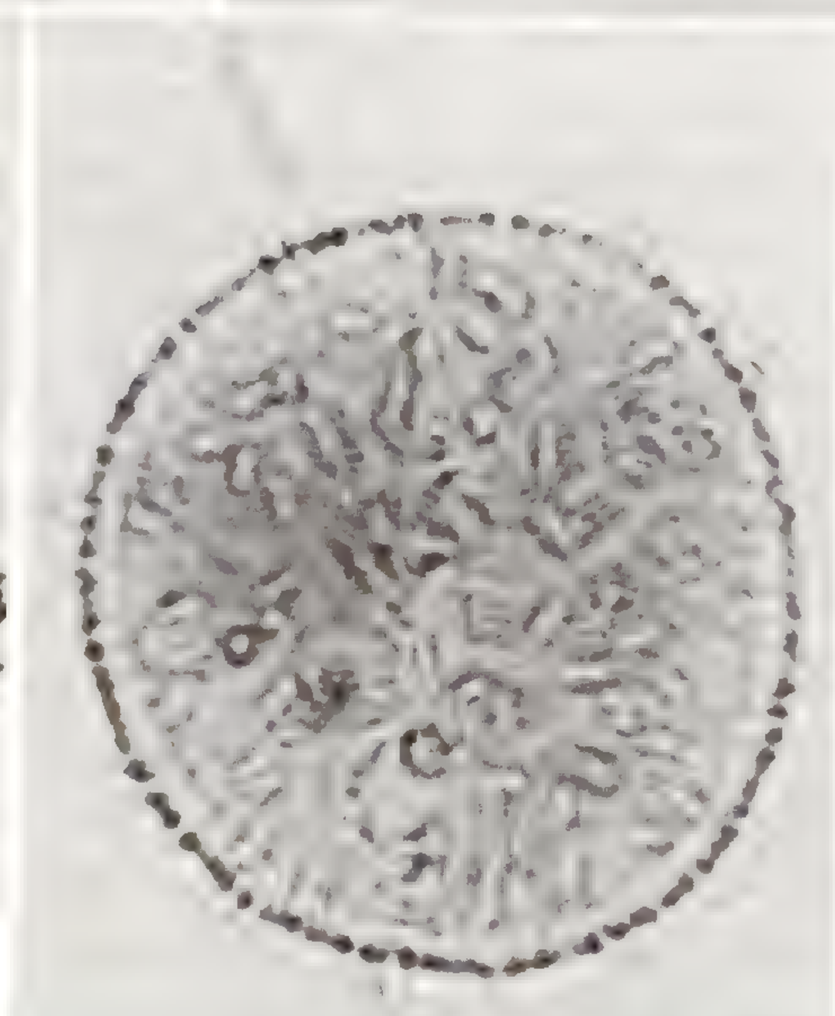
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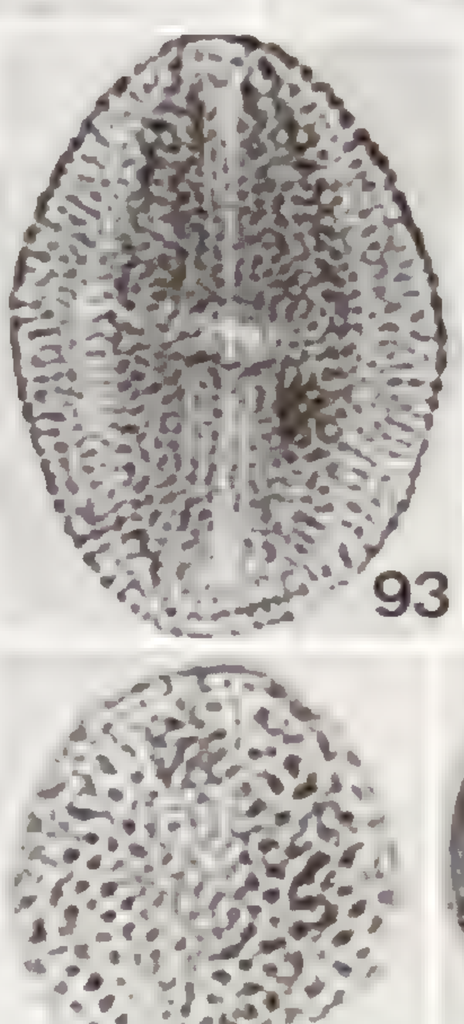
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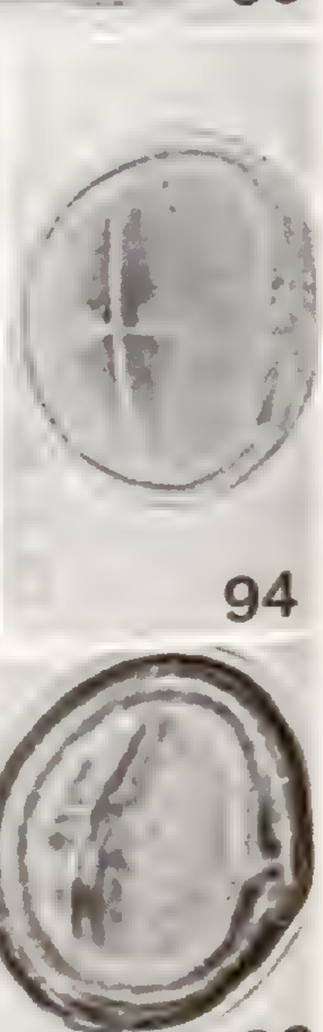
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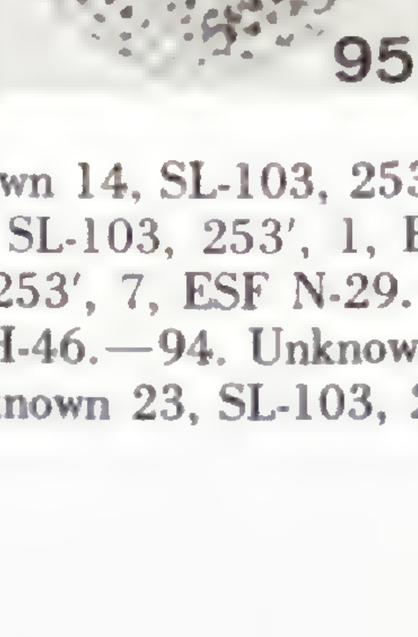
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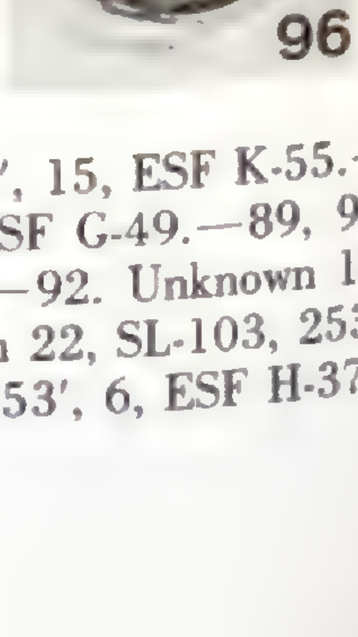
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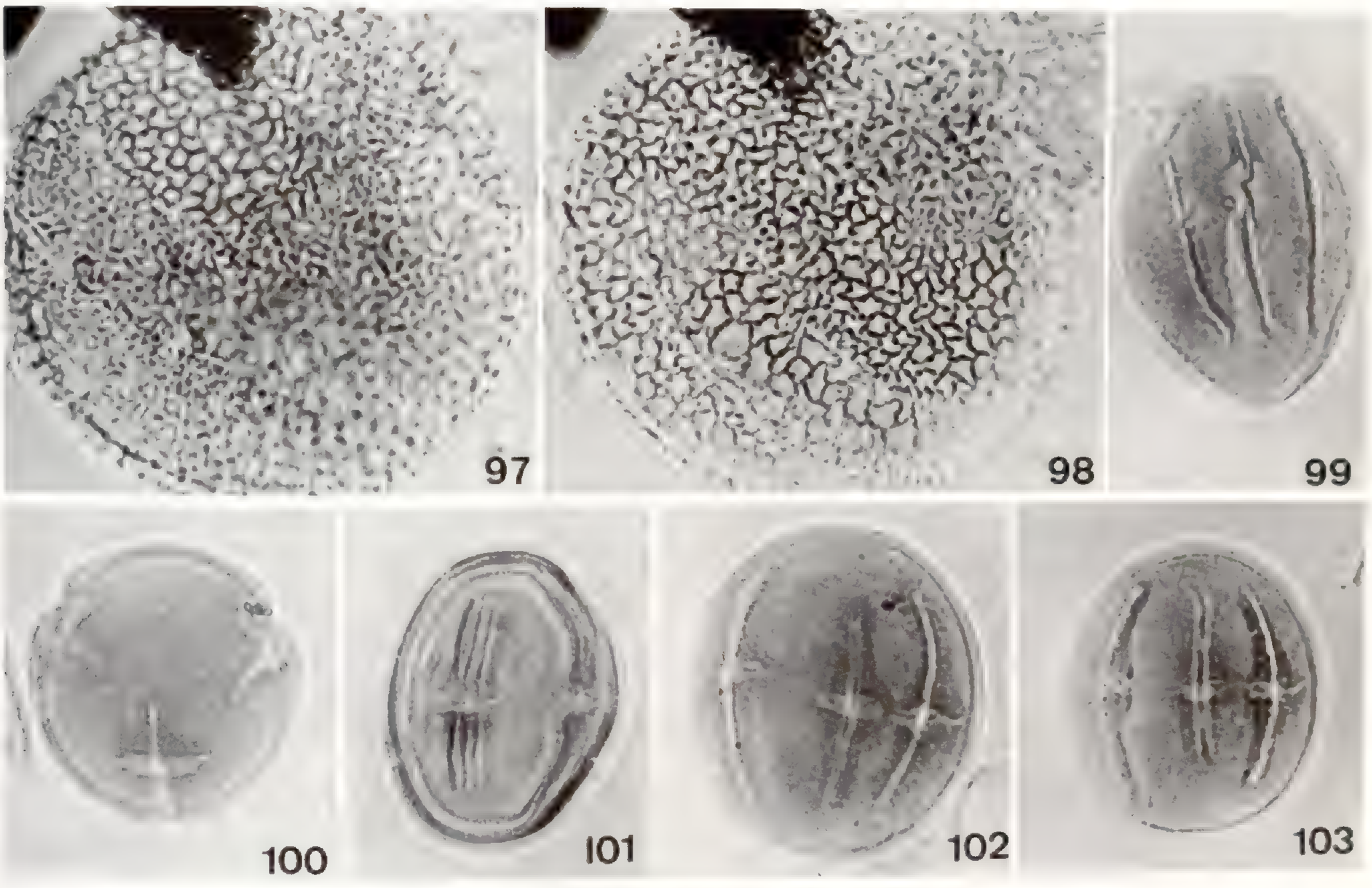
FIGURES 85–96. Fossil pollen from the Gatun Formation.—85. Unknown 14, SL-103, 253′, 15, ESF K-55.—86. Unknown 15, SL-103, 253′, 2, ESF R-36.—87, 88. Unknown 18, SL-103, 253′, 1, ESF G-49.—89, 90. Unknown 20, SL-103, 253′, 1, ESF L-35.—91. Unknown 17, SL-103, 253′, 7, ESF N-29.—92. Unknown 16, SL-103, 253′, 2, ESF T-41.—93. Unknown 24, SL-103, 253′, 13, ESF H-46.—94. Unknown 22, SL-103, 253′, 1, ESF F-36.—95. Unknown 21, SL-103, 253′, 1, ESF M-39.—96. Unknown 23, SL-103, 253′, 6, ESF H-37.



FIGURES 97–103. Fossil pollen from the Gatun Formation.—97, 98. Unknown 19, SL-103, 253′, 6, ESF G-32.—99. Unknown 27, SL-103, 253′, 2, ESF N-46.—100, 101. Unknown 25, SL-103, 253′, 1, ESF O-37; SL-103, 253′, 5, ESF K-45.—102, 103. Unknown 26. SL-103, 253′, 12, ESF P-22; SL-103, 253′, 13, ESF O-51.

straight, narrow, 22–24 μm, extending nearly entire length of grain, inner margin entire, costae colpi 3–4 μm wide, pore situated at midpoint of colpus, slitlike (1 × 4–5 μm); psilate; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 26 × 23 μm.

Unknowns 22 and 23 may represent variations of the same pollen type. The former has costae colpi that broaden at the pores, while the latter is more psilate and the wall more homogeneous.

Unknown 24 (Fig. 93). Prolate; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, narrow, 24 μm long, extending nearly entire length of grain, costae colpi 4–5 μm wide (obscure), pore situated at midpoint of colpus, elongated equatorially, 3 × 5 μm; finely reticulate, width of muri and diameter of lumina ca. 1 μm; tectate-perforate, wall 3 μm thick, individual columellae evident in median section (400× magnification); 45 × 30 μm.

These grains are similar to those of certain Anacardiaceae and Euphorbiaceae, but an exact match could not be found. They are frequent in low percentages in Gulf/Caribbean Tertiary deposits, and have been reported from the Gatuncillo, La Boca, and Paraje Solo formations.

Unknown 25 (Figs. 100, 101). Prolate; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, narrow, 20–22 μm long, inner colpus margin entire, costae colpi 3–4 μm wide, thicker at pore (4–5 μm), pores situated at midpoint of colpus, slitlike (1–2 × 4–6 μm); psilate to scabrate; tectate, wall 3 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 37–44 × 24–28 μm.

These specimens may include some tetracolporate forms and are similar to several Sapotaceae, including *Caesaria*, a pantropical genus of about 250 species. Eight were recognized for Panama by Robyns (1968), and D'Arcy (1987) listed 17 species. Most grow in moist habitats, but some range into drier premontane or tropical dry forests. Pollen of *Caesaria* includes both tricolporate and tetracolporate forms. It has been reported from the Gatuncillo, San Sebastian, Culebra, and Paraje Solo formations.

Unknown 26 (Figs. 102, 103). Prolate to prolate-spheroidal; tricolporate, colpi equatorially arranged, meridionally elongated, equidistant, straight, narrow, 21–24 μm, inner margin entire, costae colpi 3 μm wide, thicker at pores (4 μm), pores situated at midpoint of colpus, slitlike (1–2 × 3–

5 μm); psilate to scabrate; tectate, wall 2 μm thick, individual columellae just visible in median section (400× magnification); 36–41 × 33–38 μm.

Unknowns 25 and 26 are similar and may represent variations of the same pollen type. The former has slightly thicker walls and costae colpi.

Unknown 27 (Fig. 99). Prolate; tricolpate, colpi equatorially arranged, meridionally elongated, equidistant, straight, narrow, 28–30 μm long, inner colpus margin minutely dentate; scabrate; tectate, wall 2 μm thick, homogeneous to individual columellae just visible in median section (400× magnification); 42 × 30 μm.

The specimen may represent a *Quercus* grain that is slightly corroded, hence the granular appearance of the colpus margin.

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NEW TAXA OF *SOLANUM* (SOLANACEAE) FROM BRAZIL, COLOMBIA, CENTRAL AMERICA, AND VENEZUELA[1]

L. d'A. Freire de Carvalho[2]

ABSTRACT

Following morphological and taxonomic studies for a revision of *Solanum* sect. *Lepidotum*, 10 new taxa are described, not all of them in sect. *Lepidotum*: *Solanum caldense* (Brazil), *S. carautae* (Brazil); *S. davidsei* (Venezuela); *S. hatschbachii* (Brazil), *S. lepidotum* var. *lepidiochlamys* (Colombia), *S. lepidotum* var. *trianae* (Colombia), *S. oliveirae* (Brazil), *S. pereirae* (Brazil), *S. sooretamum* (Brazil), and *S. steyermarkii* (Guatemala).

A taxonomic revision of *Solanum* sect. *Lepidotum* has revealed the new species and varieties described in this paper. The morphological studies of various features of trichomes, the indumentum of the abaxial leaf surfaces, and the structure of the inflorescences as well as the realignment of the group into subsections and a new section are being published elsewhere (Carvalho & Machado, in press; Carvalho & Shepherd, in press).

Nine of the ten new taxa fall into two groups.

Section *Lepidotum* sensu strictu is identified by a suite of characters: (1) indumentum appressed-lepidote with a golden or argenteous appearance, formed of peltate and peltate-stellate trichomes; (2) inflorescence short and simple, cymose or cymose-dichotomous with a scorpioid rachis; (3) corolla campanulate-stellate; (4) flowers with pedicels articulated on the inflorescence branches; (5) anthers subsessile, oblong with large apical anterior pores and dehiscing tardily by longitudinal slits; (6) leaves geminate, discolorous with golden or argenteous indumentum on the abaxial surface. These features are shown by the new taxa *Solanum carautae*, *S. davidsei*, *S. hatschbachii*, *S. lepidotum* var. *lepidiochlamys*, *S. lepidotum* var. *trianae*, and *S. steyermarkii*.

A second group of new species shares several features: (1) indumentum lepidote-tomentose or lepidote-floccose formed of trichomes with long and ornamented stalks having lateral expansions; (2) macroscopic chaffy laminate or fringed trichomes present on branches, inflorescence, and sometimes outside the wall of the calyx; (3) inflorescence robust, short-stalked, cymose-dichotomous and with erect and pendulous rachis; (4) leaves covered by indumentum of yellowish or whitish coloration on the abaxial surface; (5) fruit globose, totally enclosed in the accrescent calyx. This group includes the new species *Solanum caldense*, *S. oliveirae*, and *S. pereirae*.

A final species, *Solanum sooretamum*, is more closely allied to *S. vellozianum* Dunal.

1. Solanum caldense Carvalho, sp. nov. TYPE: Brazil. Minas Gerais: Municipality of Caldas, 1845, *J. F. Widgren s.n.* (holotype, R ex herb. Imp. Brasil. Regnellium Mus. Bot. Stockholm). Figures 1, 8, 9, 14A, B.

Arbuscula ramis fistulosis, novellis albidis denseque floccosis pilis stellato-pedicellatis atque paleaceo-fimbriatis, brevibus mollisque. Folia ovata vel ovato-lanceolata, apice obtusa rotundataque, basi parvum attenuata, 90–110 mm lata et 170–220 mm longa, sicciata castanea, supra glabra aut glabrescentia, subtus dense lepidoto-tomentosa trichomis stellatis vel porrecto-stellatis; petiolus ad 25 mm longitudine. Inflorescentia multiflora, pendula, robusta, crassa, 90–150 mm longa, ramos rectis 60–110 mm

[1] Part of a doctoral thesis by L. d'A. Freire de Carvalho (1988). Gratitude is extended to Carlos T. Rizzini, botanist of the Botanical Garden of Rio de Janeiro, and to Pe. Clemente J. Steffen of the University of Vale do Rio dos Sinos, São Leopoldo, Estado do Rio Grande do Sul, for the Latin diagnoses, and to the curators of national (CEPEC, HB, RB, UB) and foreign (BH, F, G, K, MO, NY, P, S, W) herbaria for lending important material, including nomenclatural types. A special acknowledgment is made to W. G. D'Arcy for critical review of the English manuscript and for other help and suggestions.

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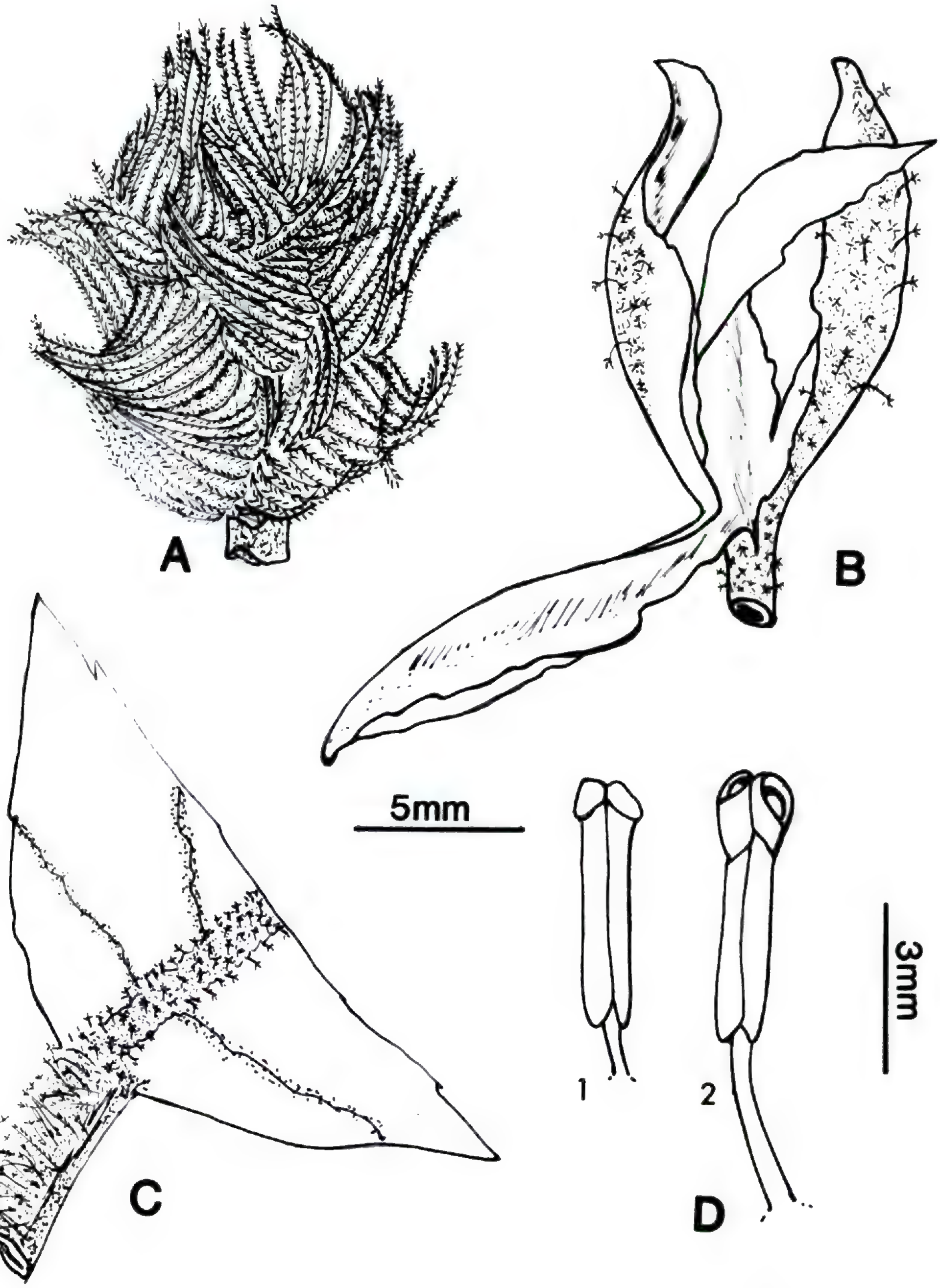

FIGURE 1. *Solanum caldense* (from *Widgren s.n.*, 1845, R).—A. Bud oblong, densely tomentose outside.—B. Corolla campanulate-stellate, densely tomentose with long-pedicellate stellate trichomes.—C. Petiole and leaf base, the petiole densely tomentose with stellate-stalked trichomes.—D. Anthers linear, the filament elongate. (1) Dorsal (abaxial) face. (2) Ventral (adaxial) face.

longis, racemosa, pedunculo 20–35 mm longo instructa. Flores globosi pubescentesque. Calyx urceolatus, externe tomentosus pilis dendriticis. Fructus haud vidi.

Small trees with fistulose branches; indumentum whitish or yellowish, densely floccose on young branches, the trichomes stellate-pedicellate, dendritic or paleaceous(chaffy)-fringed, short and soft. Leaves solitary, oblong to oblong-lanceolate, 17–22 cm long and 9–11 cm wide, glabrate above with stellate-pedicellate or rarely porrect-stellate trichomes on the main veins, densely lepidote-tomentose beneath with stellate-pedicellate ornamented trichomes, central cells present, 47–60 μm diam., 8–9(–12) radial cells 20–34 μm long, free

portion 17–32 μm; petiole ca. 2.5 cm long, densely tomentose with stellate-pedicellate trichomes. Inflorescence short pedunculate, ca. 2–3.5 cm long, extra-axillary, robust, congested, 9–15 cm long, cymose-dichotomous of about 80 flowers in series rather than glomerules, rachis straight, 6–11 cm long, densely floccose with stellate-pedicellate, dendritic and fimbriate-paleaceous trichomes; peduncle straight, 2–3.5 cm long. Flowers with buds oblong, sessile; calyx urceolate, ca. 1.6 cm long, densely tomentose outside, the lobes equal, acute, ca. 4 mm long; corolla campanulate-stellate, 2 cm long with short tube and evident vascularization, densely tomentose with long-pedicellate stellate and dendritic trichomes inside; anthers linear, ca. 5 mm long. Fruits unknown.

Paratype: BRAZIL. MINAS GERAIS: Municipality of Caldas, 1 Feb. 1876 (fl), *H. Masén 4295* (R).

Distribution and habitat. During 1841–1876 the region of Caldas in the state of Minas Gerais hosted a vegetation classified as broad-leaved tropical forest. *Solanum caldense* occurred there at that time together with *Solanum cernuum*; a more recent collection has not been seen. The flowers appear in February.

Affinity. *Solanum caldense* is similar to *Solanum pachinatum* Dunal with respect to the stellate-pedicellate, dendritic and chaffy-fringed soft trichomes, which are somewhat united like the tuft-forming, densely floccose indumentum on the branches, inflorescences, and on lower parts of the petiole It is distinguished principally by the erect, long rachis with flowers in series and by the urceolate calyx.

The species is named after the locality of Caldas, where the species was first found.

2. Solanum carautae Carvalho, sp. nov. TYPE: Brazil. Rio de Janeiro: Municipality of Parati, Parati–Mirim, 8 Dec. 1976 (fl, fr), *D. Araujo, M. D. Vianna, R. F. Oliveira & P. J. P. Carauta 1421* (holotype, GUA). Figures 2, 3D–G, 14C.

Frutex vel arbor indumento lepidoto-adpresso, trichomatibus peltatis rariusve peltato-stellatis. Folia geminata, fere conformia, membranacea, late lanceolata, 70–140 mm longa et 42–50 mm lata, indumento argenteo vel obscure cinereo pilisque peltatis in facie superiore, subtus peltatis et peltato-stellatis sparsique. Inflorescentia cymosa vel dichotoma usque ad 6.5 mm longa, pedunculo 2–3.5 mm longo, rachi brevi scorpioidea pauciflora (floribus ad 10). Fructus globosus, ad 0.9 mm diametro, calyce accrescente involucrato, indumento adpresse lepidoto ornatus.

Shrubs or trees 3–6 m tall, young branches slightly striate and angulate, the indumentum sparsely lepidote, silvery and somewhat dark with peltate trichomes. Leaves sparse, geminate, the larger leaves membranaceous, broadly lanceolate, 7–14 cm long and 4.2–5 cm wide, apically long-acuminate, almost falcate, basally attenuate, slightly asymmetric, the margin slightly inrolled, secondary veins 10–18, prominent beneath, camptodromous, discolorous, the pubescence argenteous or greenish beneath, appressed-lepidote with peltate trichomes and peltate-stellate trichomes with 8–20 radial cells, sparsely pubescent above; the smaller leaves similar but only 7 cm long; petiole ca. 1 cm long. Inflorescences opposite the leaves or extra-axillary, erect, a dichotomous cyme of ca. 15 flowers, ca. 6.5 cm long, the rachis scorpioid, 1.5–2 cm long, appressed-lepidote, the peduncle 2–3.5 cm long. Flowers with pedicels ca. 1 cm long; calyx campanulate, 2.4 mm long, the lobes acute, 1–2 mm long, appressed-lepidote outside; corolla white, rotate-stellate, 1.2 cm long and 2.5 cm diam., the lobes lanceolate, 8 mm long; anthers oblong, subsessile, 4–5 mm long, 1 mm wide, the filaments 0.50 mm free. Berry globose, ca. 9 mm diam.; fruiting pedicels erect with dense, peltate and peltate-stellate indumentum; fruiting calyx accrescent to cover most of berry, ca. 1.2 cm long, the lobes lanceolate, sparsely pubescent with peltate trichomes.

Paratype. BRAZIL. RIO DE JANEIRO: Municipality of Angra dos Reis, Ilha Grande, road to Palmas beach, 20 Apr. 1980 (fl), *M. R. V. Barbosa 31* (GUA).

Distribution and habitat. The species is a heliophyte from Atlantic forest and sandbank (restinga) of the Municipalities of Angra do Reis and Parati in the state of Rio de Janeiro.

In the "restinga" the species was observed in flower and fruit in December, and no significant variation was noticed in individuals of this shrubby plant formation.

Solanum carautae is related to *S. swartzianum* and especially to its subsp. *argyrophyllum* (Dunal) Carv., a taxon also occurring in the southern Brazilian forests of the states of Rio de Janeiro, Espírito Santo, and frequently in Minas Gerais and Bahia. It differs in its dark or silvery indumentum, its broadly lanceolate, long-acuminate leaves, which may grow to 14 cm long and have a membranaceous texture, and in its long-stalked inflorescence with scorpioid rachis.

This epithet honors botanist Pedro J. P. Carauta, researcher of the Fundação Estadual de Meio Am-

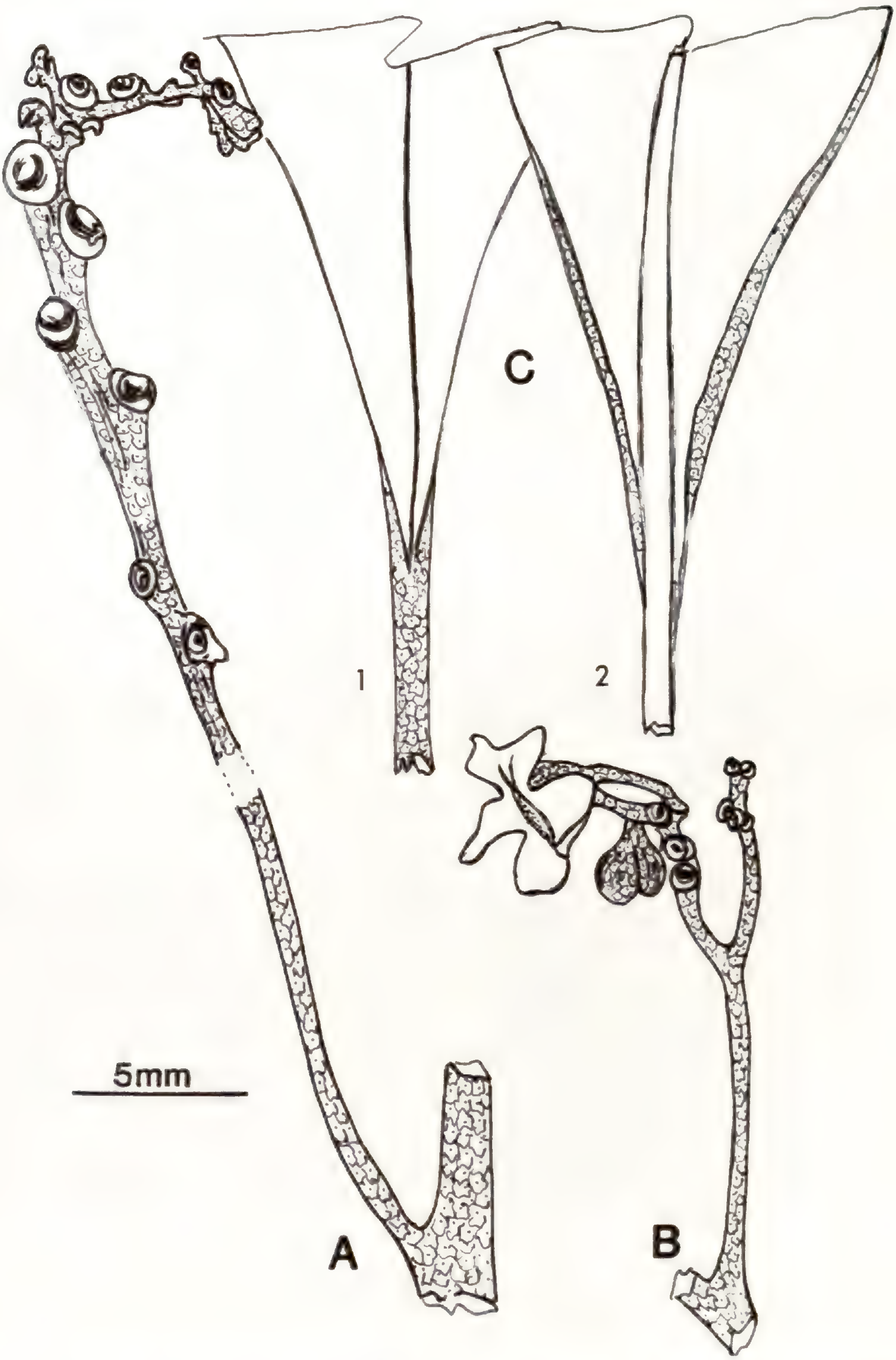

FIGURE 2. *Solanum carautae* (from *Araujo et al. 1421* GUA).—A, B. Cymose and dichotomous-cymose inflorescences, the rachis with a scorpioid cicatrice of pedicel articulations.—C. Attenuate leaf bases. (1) Ventral view. (2) Dorsal view.

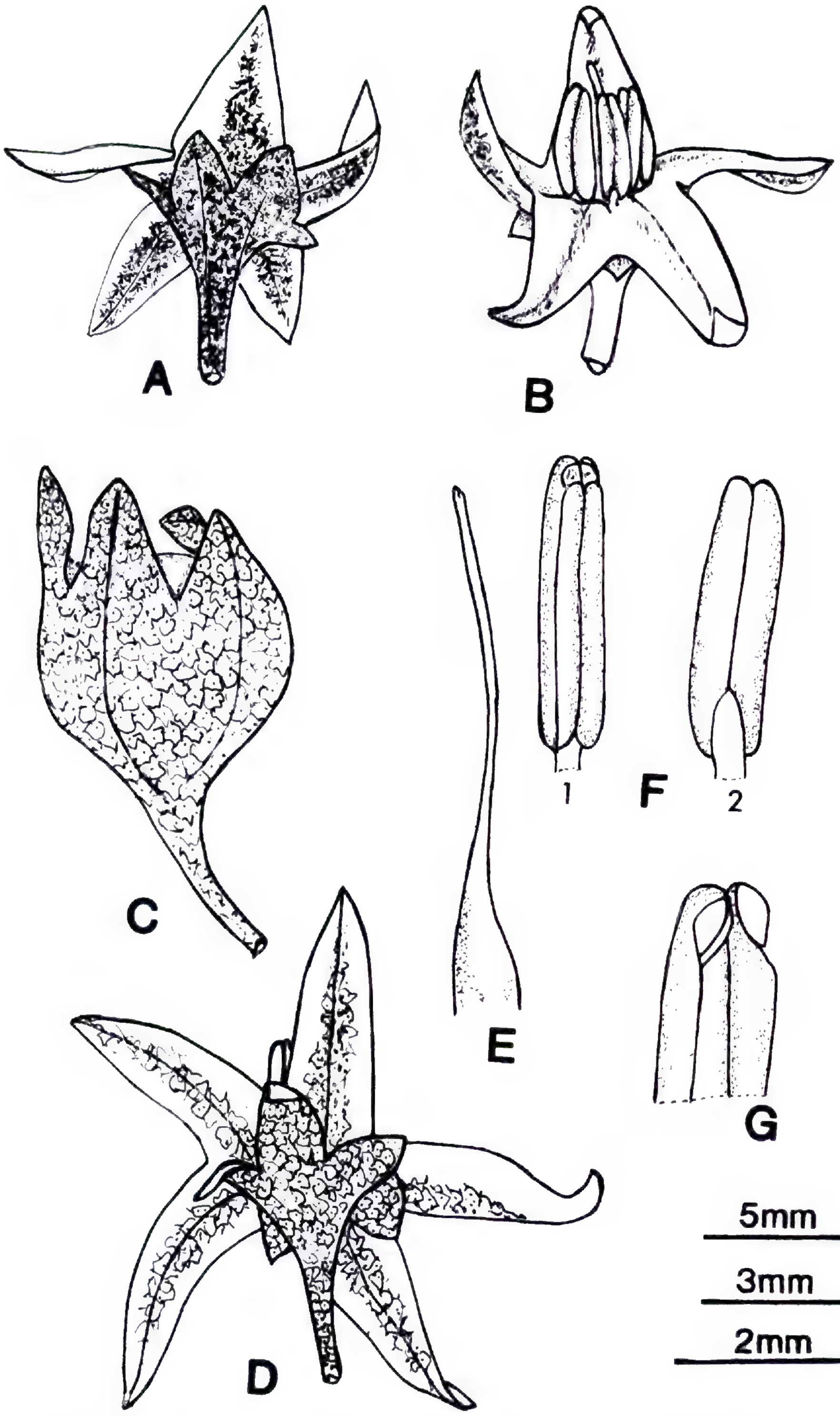

FIGURE 3. *Solanum carautae* and *Solanum hatschbachii*. A–C. *Solanum hatschbachii* (from *Hatschbach 26837* BH).—A. Open flower showing the lanceolate calyx lobes.—B. Open flower showing stamen placement.—C. Fruit, the calyx covers most of the berry. D–G. *Solanum carautae* (from *Araujo et al. 1421* GUA).—D. Open flower showing the campanulate calyx and rotate-stellate corolla with lanceolate lobes.—E. Gynoecium.—F. Stamens with oblong, subsessile anthers. (1) Ventral face. (2) Dorsal face.—G. Anther apex.

biente, Departamento de Conservação Ambiental, Rio de Janeiro (FEEMA), and one of the collectors of the type specimen.

3. Solanum davidsei Carvalho, sp. nov. TYPE: Venezuela. Bolívar: La Gran Sabana, Km 145 along hwy., 2 km S of La Ciudadella, 3 Dec. 1973 (fl, fr), *G. Davidse 4716* (holotype, MO; isotype, VEN). Figures 4, 14D.

Frutex 1.5 cm altus, indumento aurantiaco lepidoto-adpresso pilis peltatis rariusque peltato-stellatis formato, rami flexuosi, internodiis usque ad 1–5 mm longitudine. Folia geminata, inaequalia sparsa late lanceolata, apice longe cuspidata, basi acuta asymmetrica, ad 80 mm longa et 2–3 mm lata; petiolus ca. 1–2 mm longus. Inflorescentia pauciflora, in cymis simplicibus disposita, erecta, rachi valde reducta, prope 3–5; corolla alba campanulato-stellata, laciniis longe lanceolatis. Fructus calyce ampliato inclusus.

Shrubs to 1.5 m tall, the appressed-lepidote indumentum of peltate trichomes showing an intense golden color; young branches flexible and plane. Leaves unequal-geminate, sparse on branches, the internodes 1.5 cm long, the large blades broadly lanceolate, 3.5–8 cm long and 1.8–3.2 cm wide, the apex long-cuspidate or long-acuminate, the base acute, asymmetric, the margin inrolled, discolorous, glabrate or sparsely appressed-lepidote, above appressed-lepidote with peltate and peltate-stellate trichomes 35–44 μm diam. with 33–37 radial cells 16–22 μm long, secondary veins 13–15, camptodromous; smaller leaves ca. 3 cm long and 1.2 cm wide; petioles ca. 1.2 cm long, canaliculate, appressed-lepidote. Inflorescence extra-axillary, erect, ca. 5 cm long, simple cymes of 3–5 flowers with a short rachis; peduncle ca. 2.6 cm long, terete. Flowers with the pedicel terete, basally articulated, ca. 1 cm long; calyx campanulate ca. 4 mm long, the lobes acute, ca. 2 mm long, indumentum appressed-lepidote on both surfaces; corolla white, campanulate-stellate, ca. 1.5 cm long, ca. 2 cm diam., the lobes long-lanceolate, ca. 8 mm long, indumentum appressed-lepidote outside; anthers ca. 4 mm long, equal, oblong, subsessile; style with the stigmatic region spatulate. Berry globose; calyx accrescent and covering most of the berry; seeds flattened-reniform, ca. 2 mm long, 2 mm wide.

Paratype. VENEZUELA. BOLÍVAR: la Gran Sabana, 49 km W of intersection of main road to Sta. Elena and road to Cabanayen, hillside with savanna on upper slope, forest in gallery, 1,360 m, *Davidse 4752* (MO).

Distribution and habitat. This new species is indigenous to the Gran Sabana region of southern Venezuela at an elevation of ca. 1,300 m. It was found growing with dominant Gramineae of the genera *Echinolaena*, *Paspalum*, and *Trachypogon*.

Affinity. *Solanum davidsei* is closely related to *Solanum swartzianum* and especially to its subsp. *chrysophyllum* (Dunal) Carv. from Brazil and Venezuela. The two species share an intense golden appressed-lepidote indumentum and few-flowered inflorescences. *Solanum davidsei* differs from *Solanum swartzianum* subsp. *chrysophyllum* in its broadly lanceolate, long-cuspidate leaves, which occur sparsely along the flexuous branches, and in the long-pedunculate reduced rachis of the inflorescence.

4. Solanum hatschbachii Carvalho, sp. nov. TYPE: Brazil. Paraná: Municipality Bocaiuva do Sul, Sumidouro, 6 July 1971 (fl), *G. Hatschbach 26837* (holotype, BH). Figures 3A–C, 15A.

Frutex indumento lepidoto-adpresso pilis peltatis et peltato-stellatis, 17–45 cellulis radiatis interdum apiculatis constitutis. Folia geminata, inaequalia, chartacea, anguste lanceolata, ad 100 mm longa et 2.7 mm lata usque, supra indumento argenteo vel cinereo vestita subtusque glabra. Inflorescentia cymosa aut subdichotoma sive pseudo-corymbosa, usque ad 2.5 mm longa, breviter pedunculata pedunculo 1.5 mm longo rhachi scorpioidea pauciflora (floribus ad 10). Fructus incognitus.

Shrubs to 2 m tall, young branches terete and striate, indumentum argenteous or greenish, lepidote-appressed with peltate trichomes. Leaves geminate, unequal, sparse on the branches; larger leaf blades chartaceous, lanceolate, 7–10 cm long × 2–2.7 cm wide, apically acuminate, basally acute and somewhat asymmetric, the margin entire to revolute, 10–18 secondary veins prominent on the dorsal surface, camptodromous, discolorous, indumentum appressed-lepidote with peltate and peltate-stellate trichomes on the dorsal surface, glabrous above; smaller leaves to 3.5 cm long, apically obtuse. Inflorescences opposite the leaves or extra-axillary, erect, ca. 2.5 cm long, simple cymes or subdichotomous to somewhat pseudocorymbiform with ca. 10 flowers, rachis scorpioid, elongate, appressed-lepidote; peduncle short, ca. 1.5 cm long. Flowers with the pedicel articulate, to 3 mm long; buds globose; calyx campanulate, ca. 6 mm long, the lobes acute, to 4 mm long, corolla white, rotate-stellate, ca. 1.5 cm long and 2 cm diam., the lobes lanceolate, to 9 mm long, indumentum appressed-lepidote, the outside of the calyx and the corolla with peltate trichomes and their venation formed of 5 median and 10 weak laterals, hardly ramified, acropetally anastomosing; anthers equal, oblong,

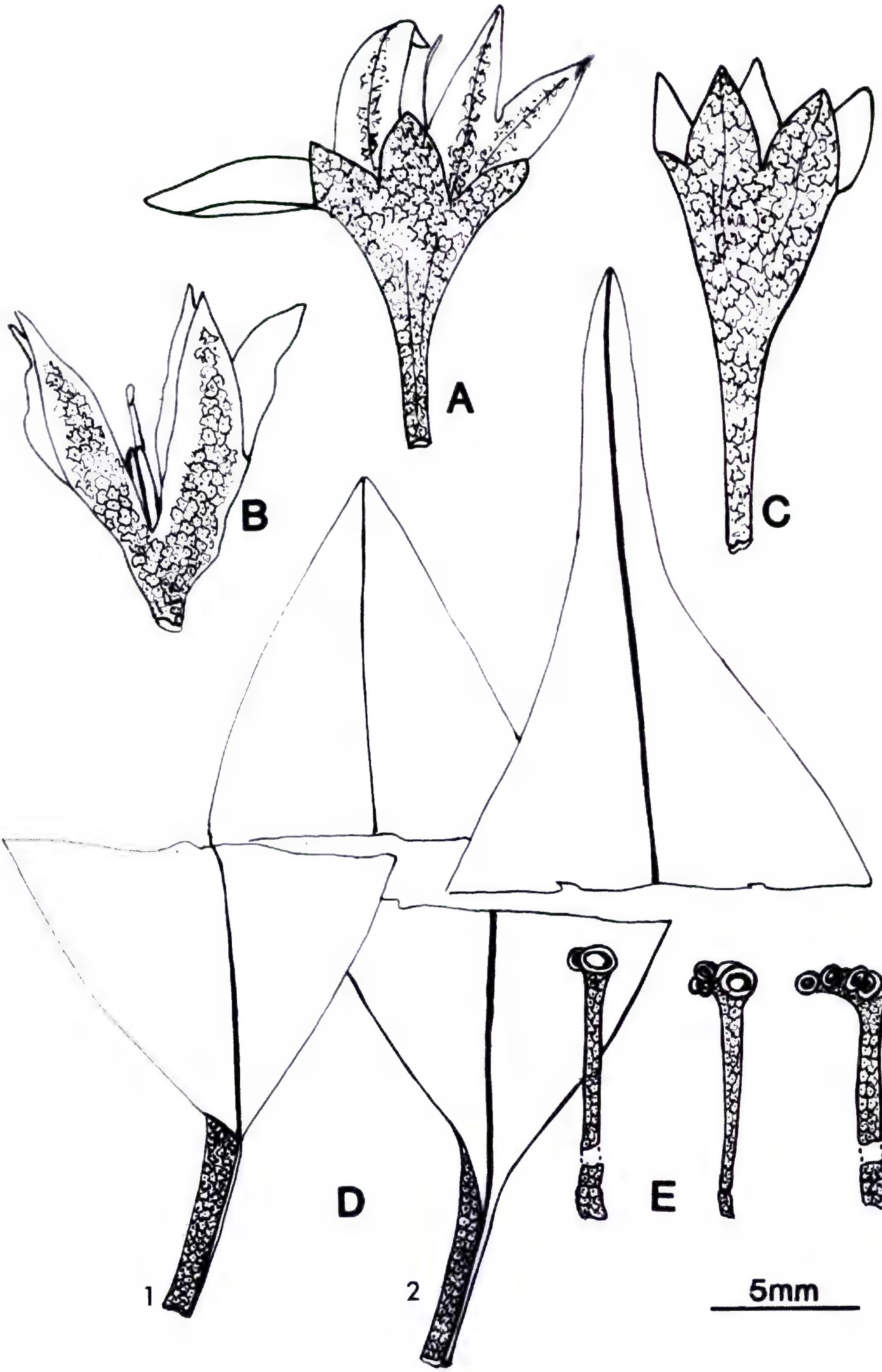

FIGURE 4. *Solanum davidsei* (from *Davidse 4716* MO).—A. Open flower showing the campanulate calyx, the campanulate-stellate corolla, and the long style.—B. Corolla showing the long-lanceolate lobes and appressed-lepidote

ca. 5 mm long, connivent, subsessile. Fruit unknown.

Paratype. BRAZIL. PARANÁ: Municipality Bocaiuva do Sul, Jaguariaíva, 10 May 1914 (fl), *P. Dusén s.n.* (S).

Distribution and habitat. This species occurs in the state of Paraná in the municipalities of Jaguariaíva and Sumidouro. The botanist P. Dusén collected it in primary forest, and Hatschbach collected it in secondary formation. Flowering, still with leaf branches, is in May and July.

Affinity. *Solanum hatschbachii* approaches *Solanum swartzianum* Roem. & Schult., especially its var. *Swartzianum*, but is distinguished by its lanceolate leaves up to 2.5 cm wide and by its leafy habit with leaves regularly spaced.

This epithet honors the collector, botanist Gert Hatschbach, from "Museu Botanico Municipal" of the Curitiba state of Paraná, a great connoisseur of the plant life of this region.

5. Solanum lepidotum var. **lepidiochlamys** Bitter ex Carvalho, var. nov. TYPE: Colombia: Cordillera Occidental, 1,900 m, 9 Sep. 1899 (fl), *E. Langlassé 58* (holotype, G; isotype, P, fragment, F). Figures 10, 15B.

Solanum lepidotum subsp. *lepidiochlamys* Bitt. mss. in sched. herb, Genève (G), nomen ined.

Arbuscula indumento adpresse lepidoto aurantiaco vestita trichomatibusque peltatis atque peltato-stellatis. Folia geminata, magnitudine formaque inaequalia, lanceolata, ca. 6 cm longa et 3 cm lata, apice recta vel falcata, basi obtusa aut decurrentia, leviter asymmetrica, margine integra et revoluta. Inflorescentia multiflora, erecta, laxa rachi scorpioidea. Fructus haud vidi.

Small trees to 3 m tall, indumentum appressed-lepidote, golden or rarely argenteous with peltate and rare peltate-stellate trichomes. Leaves geminate, unequal in size and form, the larger leaves chartaceous, lanceolate, 5.3–10 cm long and 1.5–3 cm wide, apically acuminate, straight or falcate, basally obtuse, decurrent, somewhat asymmetric, the margin entire to revolute, the indumentum appressed-lepidote above, glabrescent beneath, peltate and peltate-stellate, the trichomes, 30–47 μm diam. with 27–33 radial cells, 18–25 μm long, the free portion 2–7 μm. Inflorescence long-stalked, 5–6.5 cm long, erect, cymose-dichotomous of about 100 flowers, straight or scorpioid at the end of the rachis, ca. 2.5 cm long; peduncle ca. 30 cm long. Flowers as in the typical subspecies. Fruit unknown.

Paratypes. COLOMBIA. ANTIOQUIA: Angelopsis La Camelia, 1,800 m, 22 Jan. 1928 (fl), *Toro 884* (NY), *Mayor 401* (Z). CAUCA: El Tambo, 1,700 m, 22 July 1938 (fl), *Sneidern 1495* (S); Chisquio, Finca dos Derrumbos, 1,700 m, 3 Apr. 1949 (fl), *Asplund 10716* (NY, S); Hague, 3 Sep. 1844 (fl), *Goudot s.n.* (BM, F, MO, NY, S). VALLE: near River Calí, Pichinché, 1,700 m, 1946, *Duque-Jaramillo 3935* (NY).

Distribution and habitat. This plant grows exclusively in Colombia at 1,700–1,900 m altitude in the same place as *Solanum lepidotum* Dunal var. *lepidotum*. Flowering is in September.

Affinity. *Solanum lepidotum* var. *lepidochlamys* differs from the typical taxon, *Solanum lepidotum* Dunal var. *lepidotum*, by the lanceolate form of the leaves and the densely leafy branches.

The name of this taxon alludes to the plant's lepidote indumentum.

6. Solanum lepidotum var. **trianae** Carvalho, var. nov. TYPE: Colombia. Province Quindío: 1,800 m altitude (Nouvelle–Genade), between 1851 and 1857, *J. Triana s.n.*, Voyage de J. Triana, 1851–1857 (fl) (holotype, P; isotypes, BR, G. NY, W). Figure 15C.

Arbusculo indumento argenteo adpresse lepidoto pilis peltatis ornato. Folia solitaria et geminata inaequalia sparsa membranacea lanceolata ad oblongo lanceolata, usque ad 150 mm longa et 4.5 mm lata apice cuspidata vulgo falcata, basi obtusa margine integra trichomatibus peltatis ca. 47 μm diametro, cellulis radialibus fere ommino coalitis; petiolus ad 10 mm longus. Fructus desunt.

Trees, indumentum appressed-lepidote argenteous of peltate trichomes. Leaves sparse, solitary or geminate on young branches, unequal in size and form, the larger leaves membranaceous, from lanceolate to oblong-lanceolate, to 15 cm long and 4.5 cm wide, apically cuspidate to reflexed (falcate), basally obtuse, margin entire, trichomes peltate, ca. 47 μm diam., with ca. 35 radial cells almost totally connected; petioles ca. 1 cm long. Flowers as in the typical subspecies. Fruit unknown.

←

indumentum outside.—C. Accrescent calyx covering most of the young berry.—D. Examples of leaf bases and apices. (1) Apex acute and base acuminate. (2) Apex long-cuspidate and base acute and asymmetrical.—E. Inflorescence, simple cymes with a short rachis and terete peduncle.

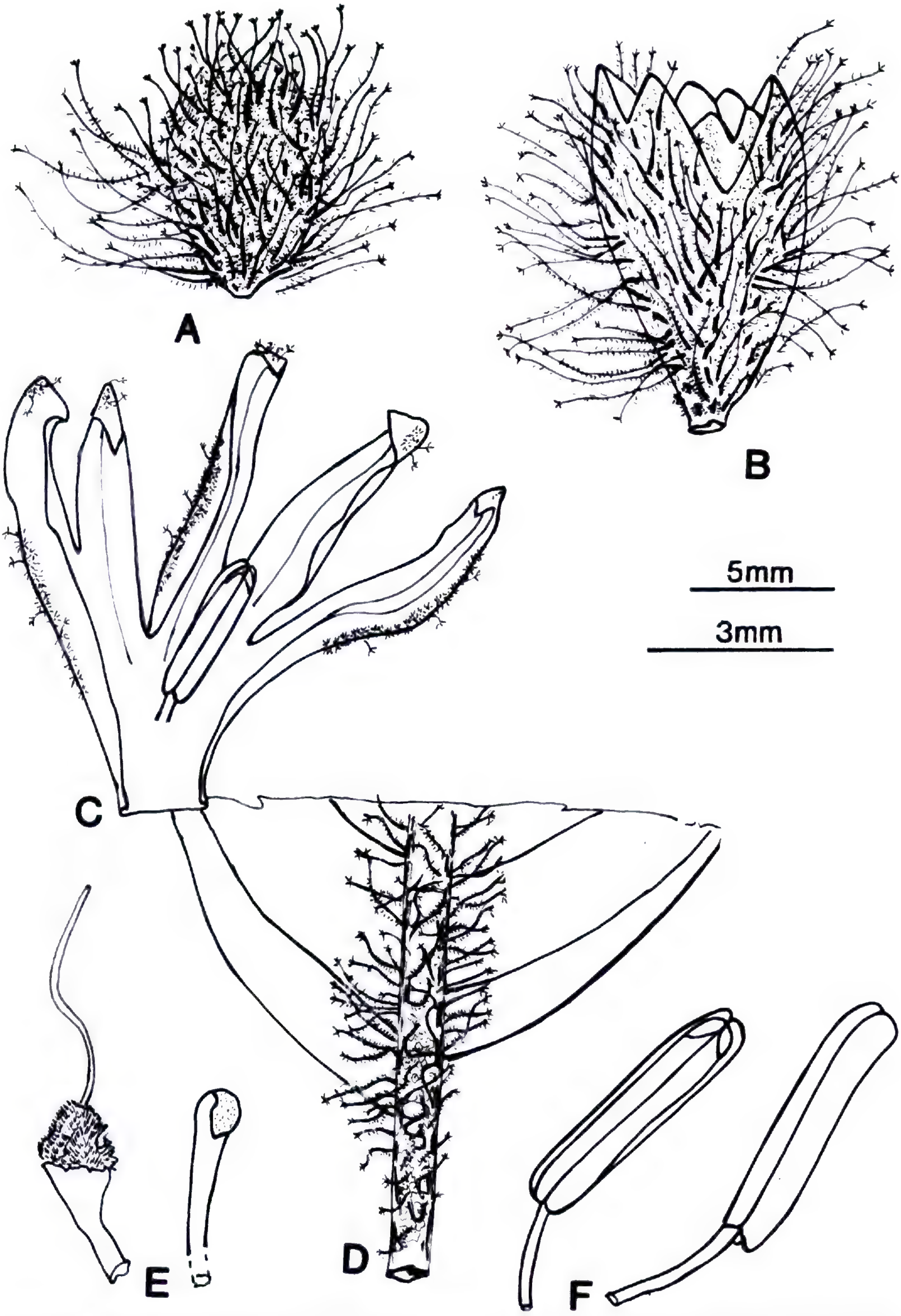

FIGURE 5. *Solanum oliveirae* (from *R. F. de Oliveira et al. 455* GUA).—A. Flower bud.—B. Flowering calyx.—C. Corolla, campanulate-stellate.—D. Leaf base and petiole apex.—E. Gynoecium showing ovary pubescence and demarcated stigmatic region.—F. Anthers, linear with elongate filaments.

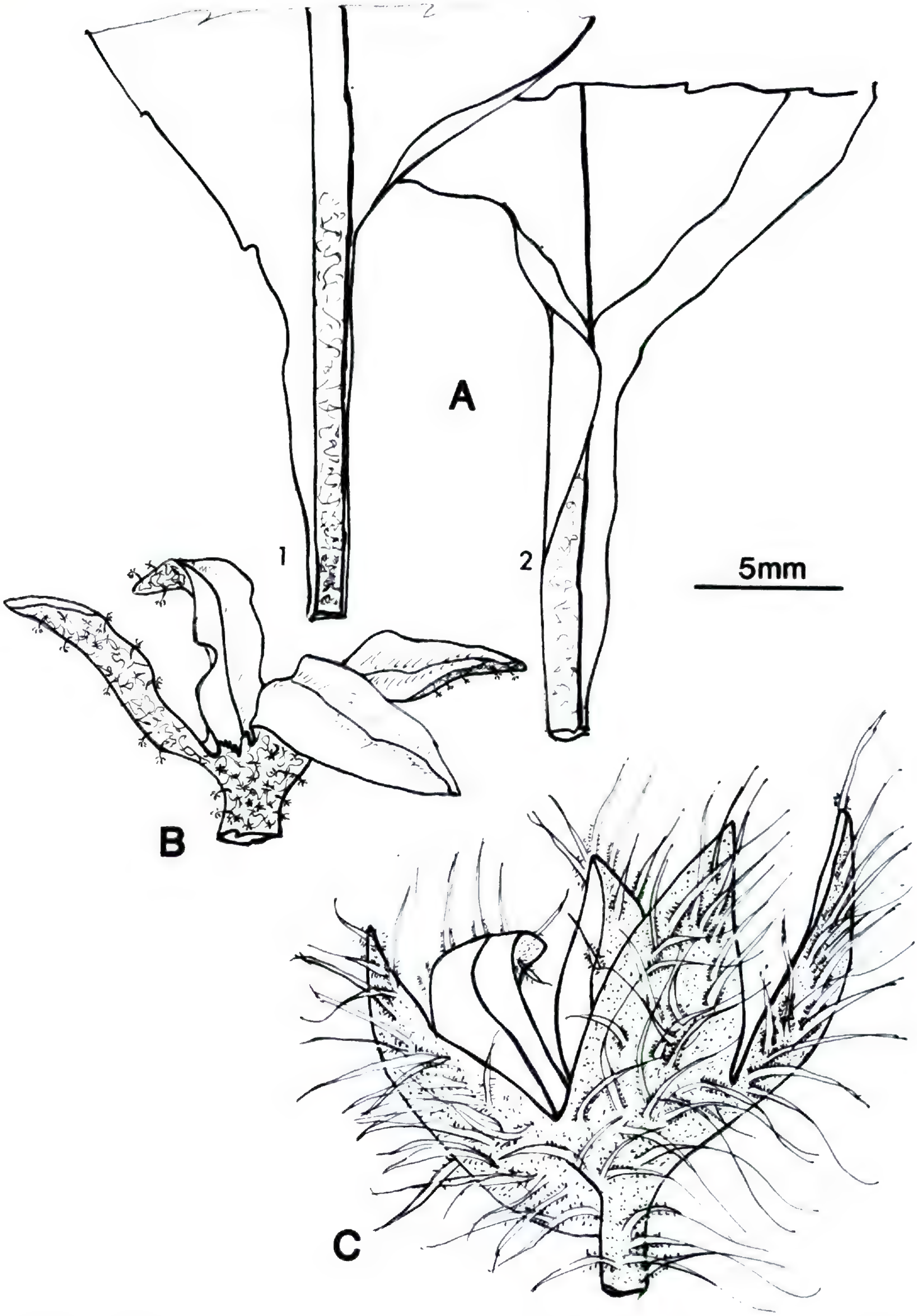

FIGURE 6. *Solanum pereirae* (from *E. Pereira 1270* RB).—A. Leaf bases. (1) Dorsal view. (2) Ventral view.—B. Corolla, campanulate-stellate.—C. Calyx, campanulate with paleaceous-laminate or fringed trichomes.

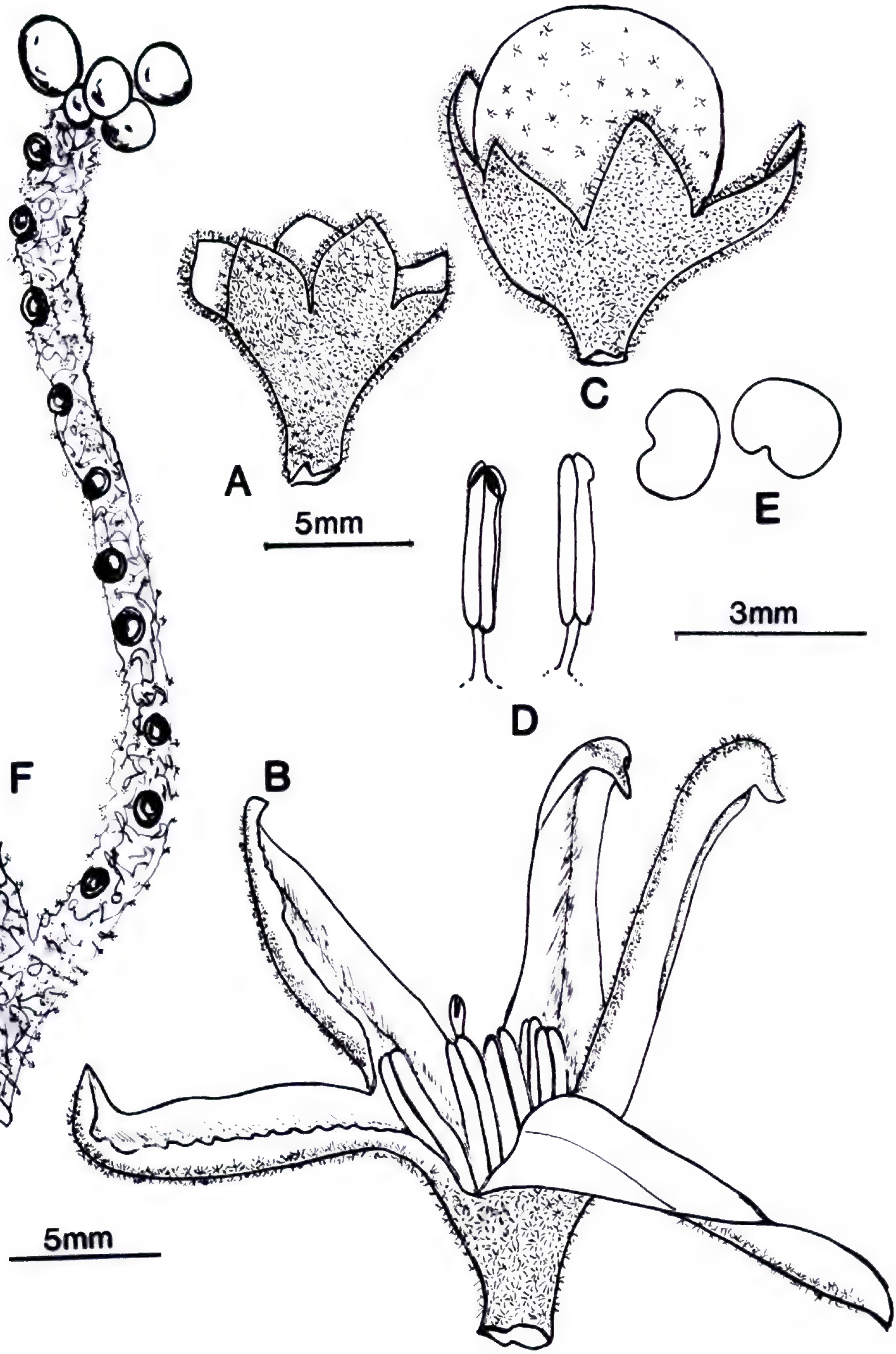

FIGURE 7. *Solanum sooretamum* (from *R. P. Belem 1534* UB).—A. Calyx, densely floccose with stellate trichomes.—B. Open corolla, campanulate-stellate with stamens and style.—C. Fruit, a globose berry partly covered by the enlarged calyx.—D. Anthers, linear with short filaments.—E. Seeds.—F. Scorpioid inflorescence branch with cicatrice of pedicel articulations.

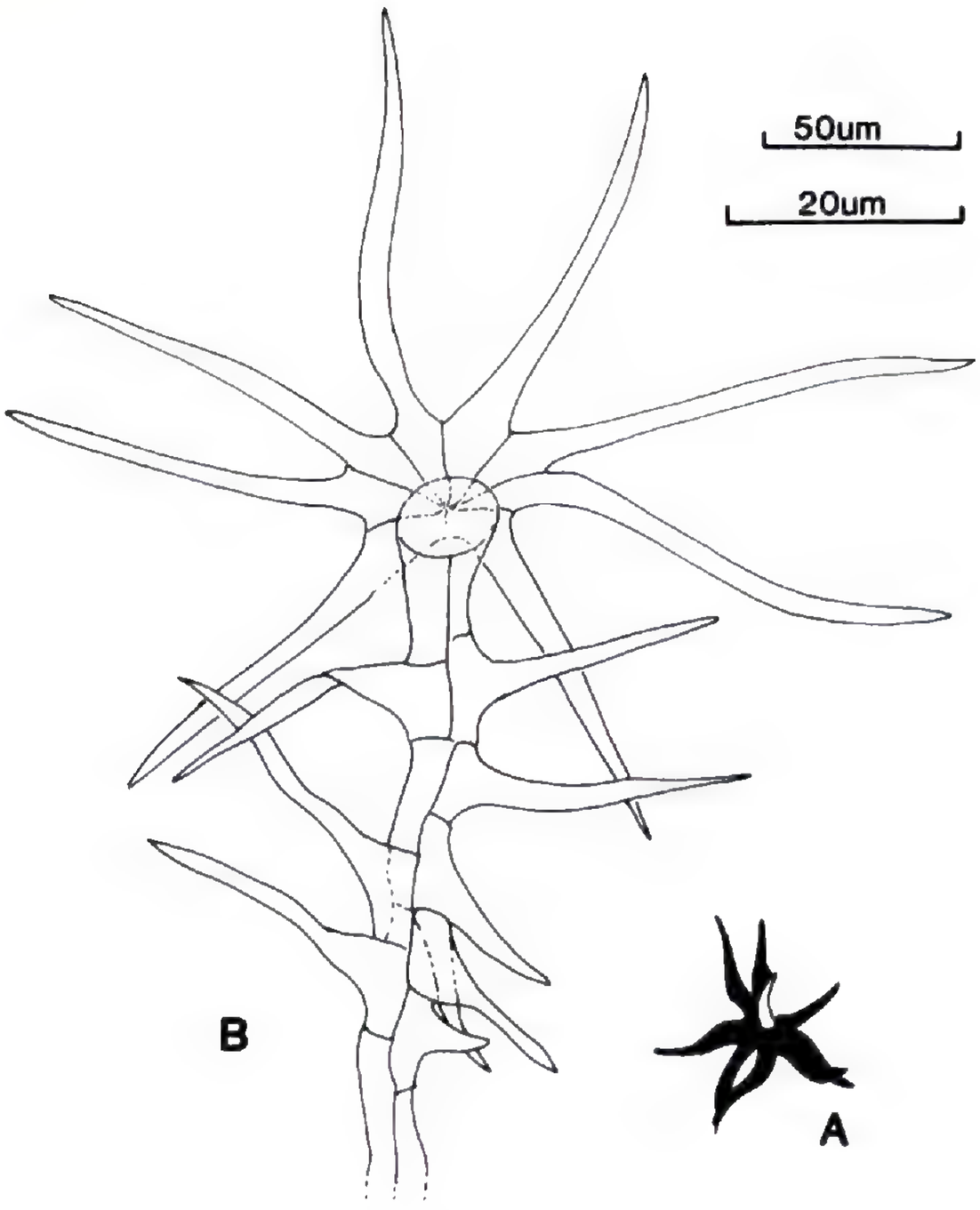

FIGURE 8. *Solanum caldense* (from *Widgren s.n.* R).—A. General view of stellate-pedicellate trichomes (50 μm scale).—B. Structure of stellate-trichome showing long stalk with lateral expansions.

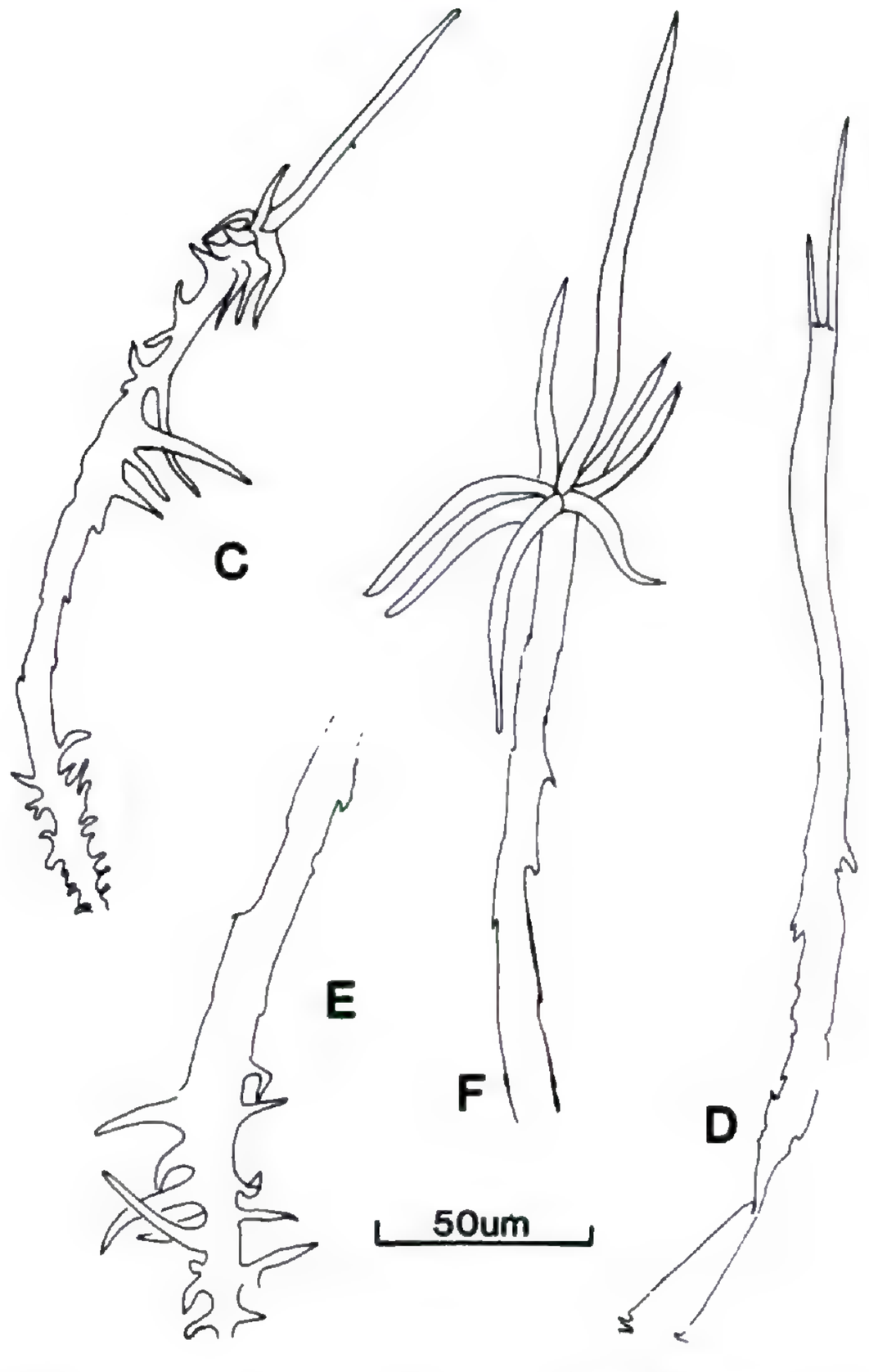

FIGURE 9. *Solanum caldense* (from *Widgren s.n.*, R).—C–F. Paleaceous-fimbriate trichomes; fringed-chaffy, stellate with a central cell, and ornamented pedicel (50 μm scale).

Distribution and habitat. The J. Triana collection was distributed to various herbaria (BR, G, NY, P, W) without indication of collection locality and sometimes with mention of only the country and altitude. This plant grows at 500–1,500 m on Quindío in the department of Huila, and it is known only by the type collection. Time of flowering is unknown.

Affinity. *Solanum lepidotum* var. *trianae* differs from the typical taxon in its argenteous indumentum, which is formed of large diameter peltate trichomes with radial cells almost totally connected and also in having a lanceolate to oblong-lanceolate leaf blade up to 15 cm long and 4.5 cm wide.

The epithet honors botanist J. Triana, collector of the type specimen.

7. Solanum oliveirae Carvalho, sp. nov. TYPE: Brazil. Rio de Janeiro: Varre–Sai, 4 Sep. 1984 (fl), *R. F. de Oliveira et al. 455* (holotype, GUA). Figures 5, 11, 16A.

Frutex ramis rigidis dense floccoso-paleaceis castaneis, pilis paleaceo-fimbriatis et dentriticis rariusve paleaceo-laminaribus vel stellatis. Folia solitaria, magna, oblonga, basi angustata, apice obtuso plus minusque emarginata, 160–260 mm longa et 90–110 mm lata, supra glabrescentia, scabra, pilis stellatis, infra pallidiora, cinerascentia, dense lepidoto-tomentosa, pilis stellatis raris ornata secundum nervos; petiolus ca. 30 mm longus. Inflorescentia extra-axillaris, cymosa dichotoma, ramis rectis, singulis ramis floribus prope 30, indumento densissimo floccoso-paleaceo castaneo vestita ab omni parte, pilis paleaceo-laminaribus atque fimbriatis brevibus flores non cingentibus. Flores lutei. Calyx urceolatus vel late tubulosus, strigosus. Bacca globosa, calyce ampliato inclusa.

Shrub 2–6 m tall with rigid or fistulose branches, the indumentum whitish or yellowish, densely floccose, chaffy-fringed of dendritic and rarely chaffy-laminate and stellate trichomes with multicellular pedicels. Leaves solitary, oblong, 16–26 cm long and 9–11 cm wide, apically obtuse to obtuse-emarginate, basally obtuse, glabrescent above with stellate pedicellate trichomes bearing an apiculate central cell 66–72 μm diam., (5–)8 radial cells, 30–39 μm long and the free portion 25–36 μm; densely lepidote-tomentose beneath with stellate trichomes 35–44 μm diam. having 14–16(–17) radial horizontal cells, 16–21 μm long, the free portion 10–16 μm long, short-stalked, ornamented with a small apiculate central cell, rarely with soft, hyaline stellate trichomes that have ca. 20 radial cells and multiseriate pedicels on the main veins; secondary

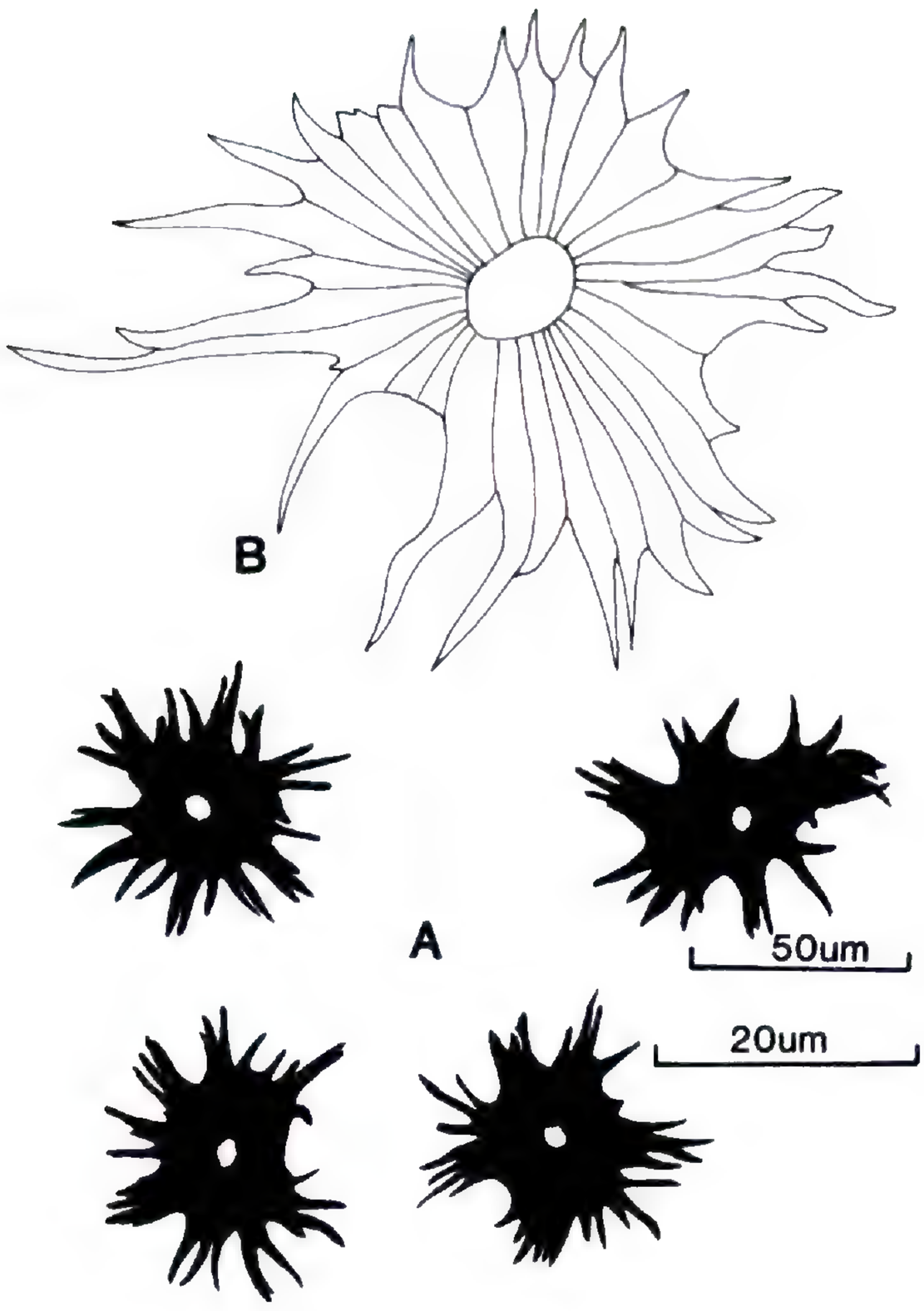

FIGURE 10. *Solanum lepidotum* var. *lepidiochlamys* (from *Langlassé 58* G).—A. General view of stellate trichomes (50 μm scale).—B. Structure of the trichome (20 μm scale).

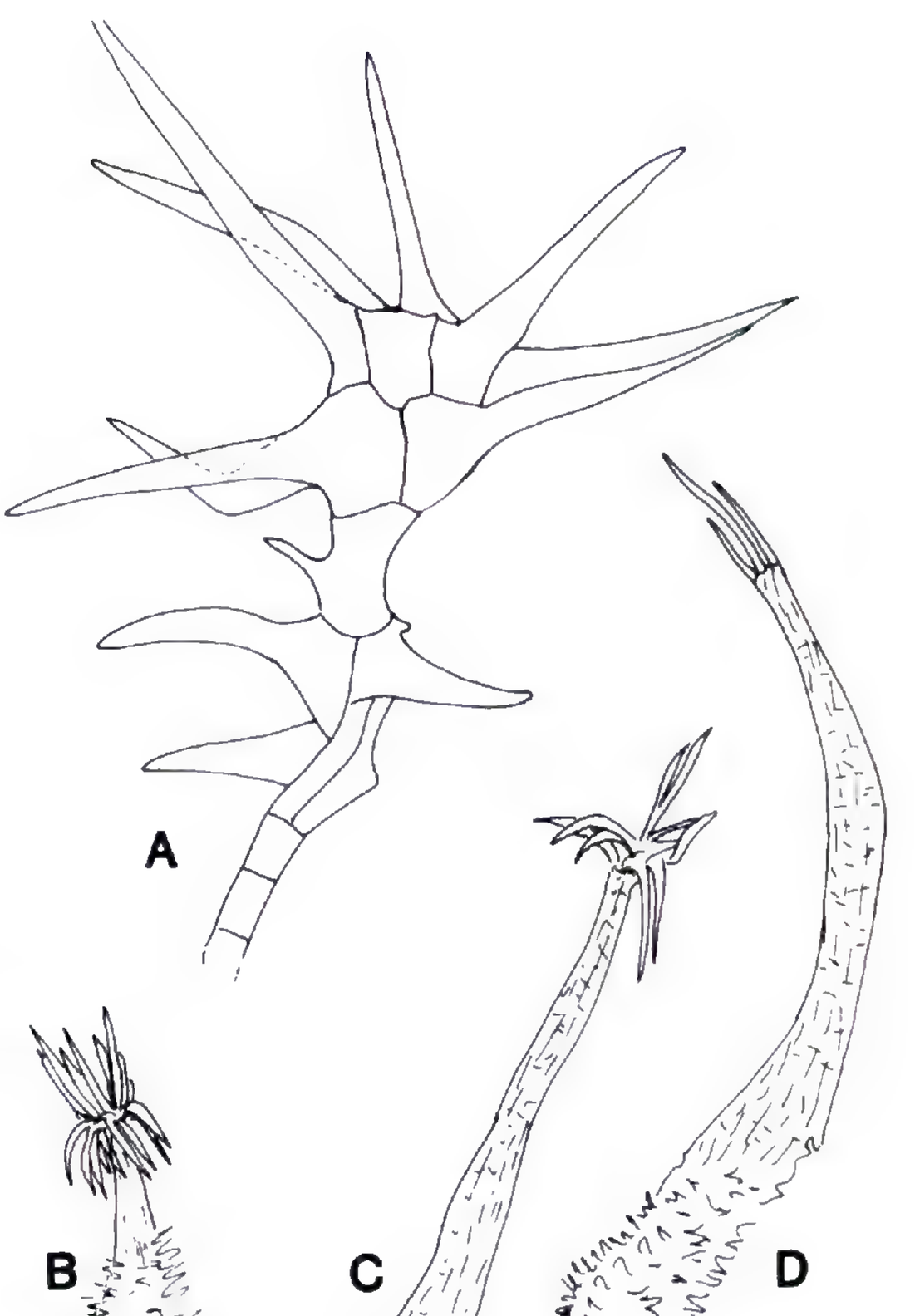

FIGURE 11. *Solanum oliveirae* (from *R. F. de Oliveira et al. 455* GUA).—A. Structure of dendritic trichome with uniseriate pedicel (20 μm scale).—B–D. Paleaceous-laminar trichomes, the apical cells tufted and the base ornamented (50 μm scale).

veins 15–18; petiole 1.2–5 cm long, densely floccose-chaffy, laminate and fringed-chaffy (laminate), and dendritic trichomes. Inflorescence extra-axillary, pedunculate, robust, congested, 14–17 cm long, cymose-dichotomous of about 30 flowers in series rather than glomerules, the straight rachis densely floccose, paleaceous, with short-laminate and fimbriate trichomes that do not involve the flowers; peduncle straight, ca. 3 cm long, chaffy-laminate. Flower buds oblong, 5–6 mm long; pedicels ca. 3 mm long; calyx urceolate or broadly tubular, longer than 1 cm, strigose, chaffy-fringed outside, short, rigid, the lobes equal, acute, ca. 2 mm long; corolla campanulate-stellate, ca. 2.5 cm long, the lobes equal, ca. 1.5 cm long, the tube short, ca. 3 mm long, pubescent outside with stellate trichomes having ca. 8 radial cells, and also trichomes with ca. 8 radial cells that are rarely stellate multiseriate; anthers linear, ca. 6 mm long, subsessile; style ca. 1.4 cm long, the stigmatic region demarcated by papillae. Berry globose, ca. 1 cm diam., enclosed in the expanded calyx.

Paratypes. BRAZIL. Without other locality, *Regnell III 977* (fl, fr) (S). ESPÍRITO SANTO: Mimoso, 1916, *Souza Brito 149* (fl) (R). RIO DE JANEIRO: Cacimbas near River Itabapaoana, Sep. 1909, *Sampaio 906* (R); fields, Bonsucesso farm, Mar. 1918, *Sampaio 2864* (R); Petrópolis, Serra da Estrela, *Riedel 14123* (fl) (NY). SÃO PAULO: Reserva do Parque Estadual das Fontes do Ipiranga, 3 Feb. 1983 (fl, fr), *Macedo 13* (SP).

Distribution and habitat. The yellow flowers, which are infrequent in this group, were indicated only for the holotype, collected in the state of Rio de Janeiro. Plants flower in February, March, and September. The species has been collected only in tropical humid forest in the states of Espírito Santo and Rio de Janeiro.

Affinity. *Solanum oliveirae* is distinguished from the similar *Solanum cernuum* by length of the chaffy-laminate indumentum of the inflorescence, which is shorter than the flowers so that the flowers are evident. The strigose aspect of the chaffy-laminate covering on the outside of the calyx, the short and floccose pubescence types on stems and branches, as well as the shape and con-

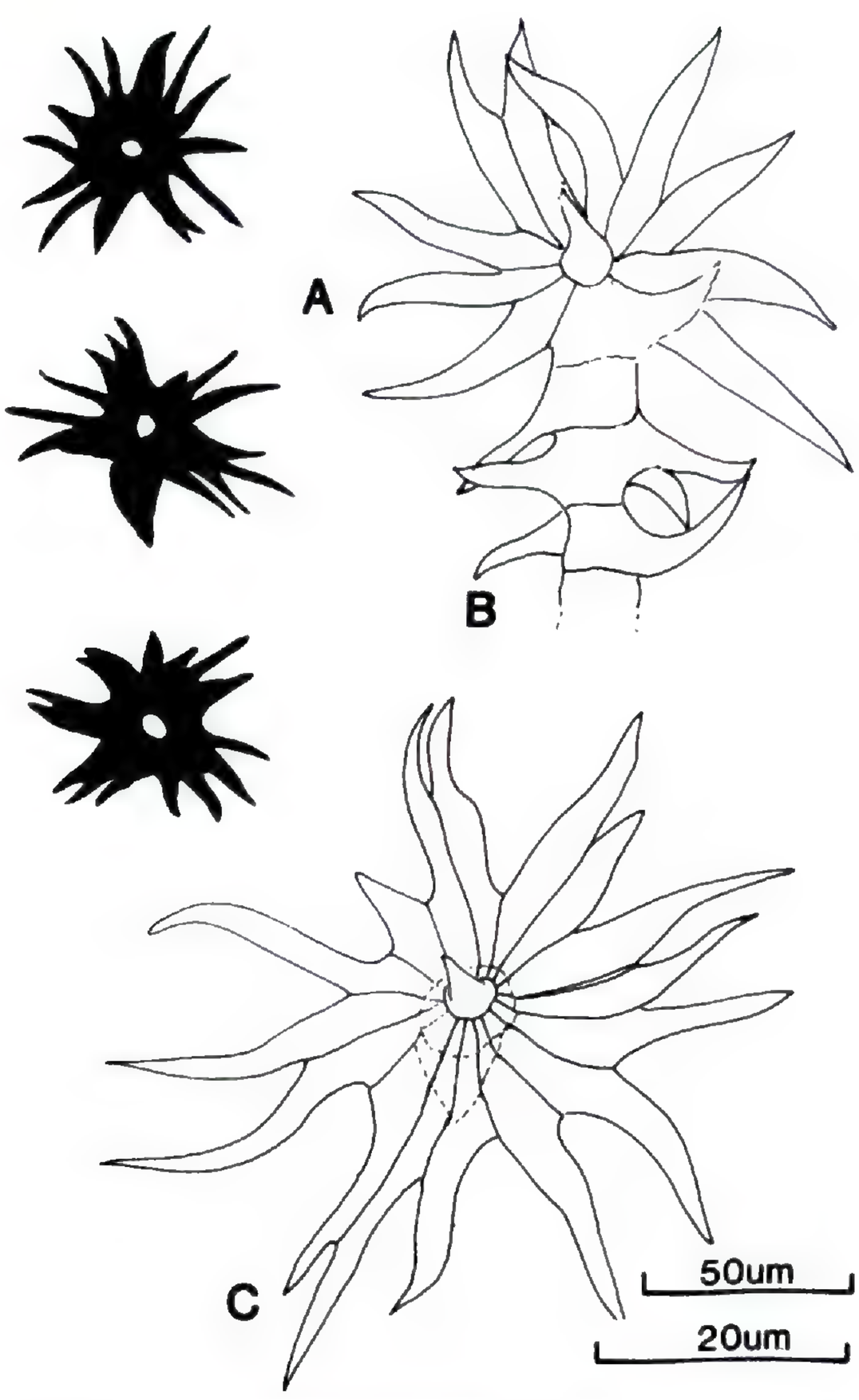

FIGURE 12. *Solanum pereirae* (from *E. Pereira 1270* RB).—A. General view of peltate trichomes (50 μm scale).—B. Structure of peltate trichome (20 μm scale).—C. Structure of peltate-stellate trichome (20 μm scale).

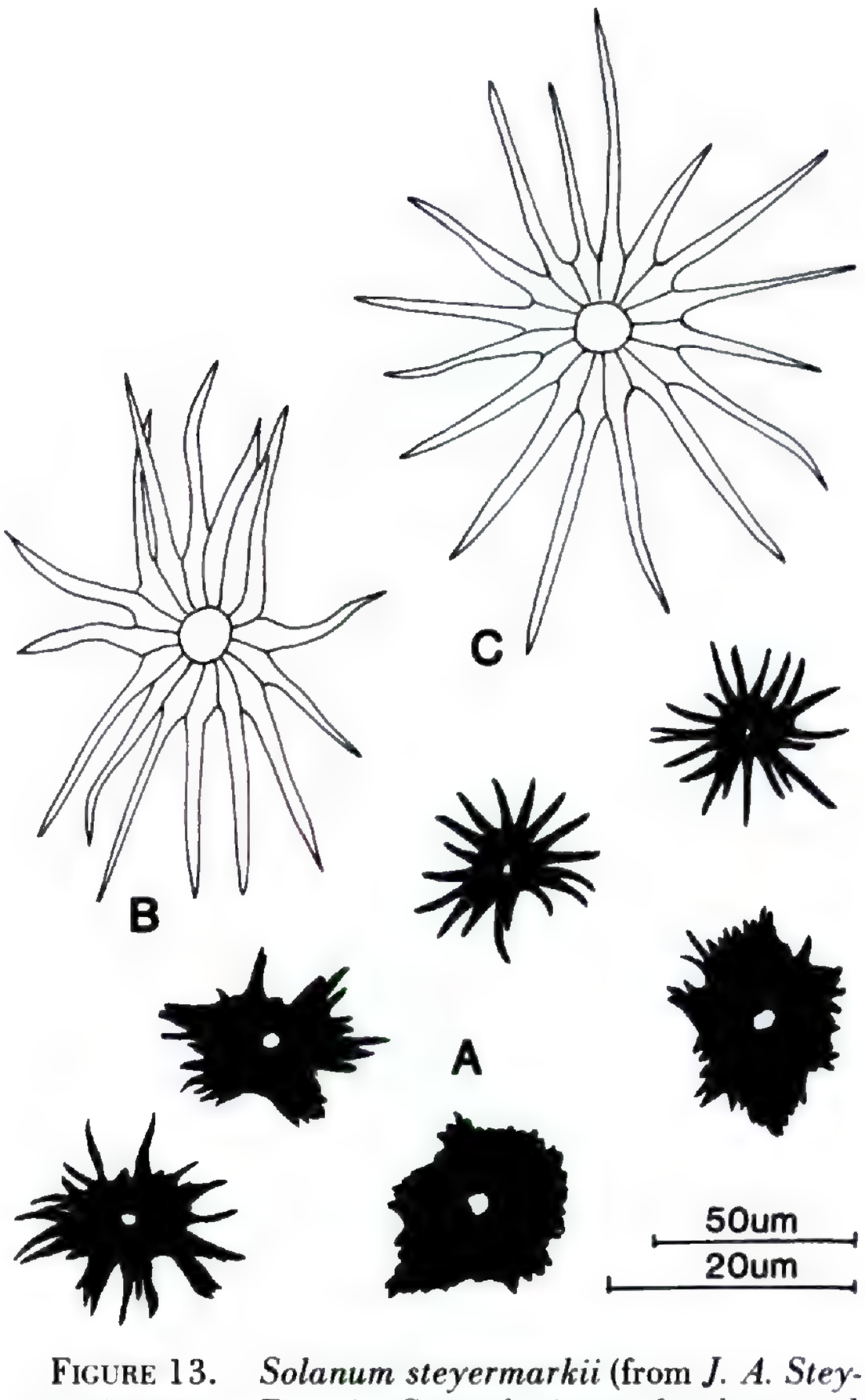

FIGURE 13. *Solanum steyermarkii* (from *J. A. Steyermark 33825* F).—A. General views of peltate and peltate-stellate trichomes (50 μm scale).—B. Structure of peltate trichome (20 μm scale).—C. Structure of peltate-stellate trichome (20 μm scale).

sistency of the leaves, are the main distinctions of this species.

The epithet honors botanist Ronaldo F. Oliveira, Fundação Estadual de Engenharia do Meio Ambiente, Departamento de Conservação Ambiental, Rio de Janeiro (FEEMA), a member of the group that collected the type specimen.

8. Solanum pereirae Carvalho, sp. nov. TYPE: Brazil. Rio de Janeiro: Municipality of Santa Maria Madalena, Tamandaré, 18 Mar. 1955 (fl), *E. Pereira 1270* (holotype, RB). Figures 6, 12, 16B, C.

Arbuscula ramis rigidis aut fistulosis, novellis subangulosis, dense floccoso-castaneis trichomatibus elongatis paleaceis, laminaribus fimbriatisque, dendriticis, rarissime stellato-peltatis pedicelis multicelullaribus. Folia solitaria magna, lanceolata ad late lanceolata, in facie superiore glabra, in inferiore squamosa sive squamato-tomentosa, castanea, pilis peltato-stellatis, porrecto-stellatis supra nervum medium insertis; petiolus floccoso-tomentosus, trichomatibus stellatis pedicellatisque, dentriticis raro fimbriatis. Flores cymosi, congesti, extra axillares cymis 1–3 ramosis, ramis pendulis; trichomata longa laminacea; pedunculus cymarum pubescens. Calyx campanulatus, extus paleaceus, pilis stellatis aut fimbriatis vestitus. Fructus ignotus.

Shrub 3–3.5 tall, young branches plane, indumentum brownish, appressed-lepidote with peltate-stellate trichomes having a multicellular pedicel. Leaves solitary, lanceolate to broadly lanceolate, 14–40 cm long and 6.5–12(–20) cm wide, apically acuminate, basally obtuse-rotund to asymmetric; glabrescent above, densely appressed-lepidote beneath with peltate-stellate trichomes, 35–39 μm diam. with 15–16 radial cells, 15–17 μm long, the free portion 7–13 μm, the central cell apiculate, also with chaffy-fringed trichomes that are rarely peltate-multiseriate; secondary veins 14–20; petiole 1.5–4 cm long, appressed-lepidote, the stellate trichomes with ornamented long stalks. Inflorescence robust, extra-axillary, pedunculate, 8–20 cm long, cymose-dichotomous, flowers in series, rarely congested, the rachis straight, 3–4-branched, ca. 6 cm long, densely paleaceous, with long, laminate

FIGURE 14. *Solanum caldense*, *S. carautae*, and *S. davidsei*. a, b. *Solanum caldense* (from *Widgren s.n.* R).—a. Habit.—b. Portion of cymose-dichotomous inflorescence with straight rachis.—c. *Solanum carautae*. Habit with flower and fruit.—d. *S. davidsei*. Habit with flowers and fruit.

FIGURE 15. *Solanum hatschbachii*, *S. lepidotum* var. *lepidiochlamys*, *S. lepidotum* var. *trianae*, and *S. oliveirae*.—a. *Solanum hatschbachii* (from *Hatschbach 26837* BH). Habit with flowers.—b. *Solanum lepidotum* var. *lepidiochlamys* (from *Langlassé 58* G). Habit with flowers.—c. *Solanum lepidotum* var. *trianae* (from *Triana s.n.* P). Habit with flowers.—d. *Solanum oliveirae* (from *Oliveira et al. 455* GUA). Habit with cymose-dichotomous flowering.

trichomes enveloping the flowers; peduncle ca. 3 cm long, chaffy-laminate. Flowers with buds oblong, 2–4 mm long; pedicel ca. 3 mm long; calyx campanulate, ca. 2 cm long, pubescent with stellate trichomes with ornamented stalks and paleaceous-laciniate or fringed trichomes outside, the lobes ca. 7 mm long; corolla campanulate-stellate, ca. 2 cm long, ca. 2 cm diam., with trichomes with ornamented stalks, the lobes ca. 1 cm long; anthers linear, ca. 3 mm long, subsessile, the filaments ca. 1 mm long; ovary globose, tomentose, ca. 9 cm long. Fruit unknown.

Paratypes. BRAZIL. ESPÍRITO SANTO: near Domingos Martins, S. Miguel, 8 Feb. 1973 (fl), *Hatschbach 31386* (BH, C, R). PERNAMBUCO: May 1978 (fl), *Burle-Max s.n.* (RB). RIO DE JANEIRO: Municipality of Santa Maria Madalena, *Lisboa s.n.* (fl) (RB); farm Mater Bem, 18 Feb. 1981 (fl), *G. Martinelli et al. 7610* (K, MO, RB); *Martinelli et al. 7610* (fl) (K, MO, RB); 24 Nov. 1977 (fl), *Mautone 449* (RB); road to Pedra da Agulha, 7 Mar. 1978 (fl), *M. C. Viana et al. s.n.* (GUA, HB); Serra de Estrela, 14 May 1864, 22 June 1873, *Glaziou 1077, 6658* (fl) (both P).

Distribution and habitat. This plant grows in the forested parts of the city of Santa Maria Madalena, flowering in February and March.

Affinity. *Solanum pereirae* is similar to *Solanum cernuum* but differs in its long chaffy-laminate trichomes, which are present only on the branches of the inflorescence. It is also suggestive of *Solanum vellozianum* because of the brownish appressed-lepidote tomentum of the leaf undersides.

The epithet honors Edmundo Pereira, researcher at the Botanical Garden of Rio de Janeiro, collector of the type specimen, a great student of the plant life of Brazil, and a teacher of systematic botany.

9. Solanum sooretamum Carvalho, sp. nov. TYPE: Brazil. Espírito Santo: Forest Reserve of Sooretama, 9 Aug. 1965 (fl), *R. P. Belem 1534* (holotype, UB; isotype, CEPEC). Figures 7, 17A, B.

Arbuscula ramis rigidis aut fistulosis juventude subangulatis, castaneis, tomentosis vel floccosis trichomatibus stellatis pedicellis longis lateraliter expansis, dentriticis fimbriatisve. Folia lanceolata, basi leviter cuneata, 100–430 mm longa et 50–160 mm lata, supra glabra vel glabrescentia subtusque dense lepidoto-tomentosa colore castaneo imbuta; petiolus 13–40 mm longus. Inflorescentia cimoso-corymbosa, multiflora, longius pedunculata, erecta, floccosa pilis stellatis pedicellatis lateraliter excrecentibis ornatis; rachis apicem versus scorpioidea. Flores subsessiles. Calyx campanulatus, extus floccoso-stellatus, 59 mm longus. Corolla ad 9 mm longa et ca. 20 mm diametro. Bacca globosa puberula, laciniis calycis inaequalibus paullo supra medium circumvallata.

Small tree to 6 m tall, young branches ca. 6 cm diam., subangulate, striate and fistular, indumentum brownish, appressed-lepidote and lepidote-tomentose to densely floccose, peltate-stellate, trichomes large, dendritic and chaffy-fringed, with an apiculate central cell and a long or short pedicel with lateral projections. Leaves solitary, not geminate, lanceolate, 10–43 cm long and 5–16 cm wide, apically acute or sometimes attenuate at both ends, basally cuneate, the margin entire, secondary veins 16–40, prominent beneath, camptodromous, discolorous; brownish above, glabrate; beneath densely lepidote-tomentose with peltate-stellate trichomes, 41–46 μm diam. having 16–17 radial cells 15–20 μm long, the free portion 9–14 μm long; petiole lepidote-floccose, 1.3–4 cm long. Inflorescence erect, extra-axillary, opposite the leaves or pseudoterminal, corymbiform cymes ca. 10–35 cm long, with scorpioid branches up to 3rd order, rachis elongate, ca. 6 cm long, scorpioid at the ends, each with more than 50 flowers; tomentose to densely floccose, with stellate trichomes having lateral expansions on the long stalks and with large fringed-chaffy trichomes; peduncle erect, terete to flattened-angulate, to 9–15 cm long. Flowers with the buds oblong, 4 mm long; pedicel obsolete or short, basally articulated; calyx campanulate, to 9 mm long, densely floccose with stellate trichomes outside; pedicel articulate subsessile; corolla white, campanulate-stellate, to 1.5 long and 2 cm diam., the lobes lanceolate, to 9 mm long, floccose; anthers linear to linear-oblong, ca. 4 mm long, equal, the filaments ca. 1 mm long. Berries globose, ca. 1 cm diam., the fruit walls with sparse peltate-stellate trichomes, partly covered by the enlarged calyx; seeds ca. 23, 4–5 mm long, the testa little-ornamented, striate-reticulate. Sclerocytes (stone cells) globose or somewhat deltoid geminate, ca. 2 mm long, slightly rugose on the surface, adherent inside the wall fruit apex.

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FIGURE 16. *Solanum oliveirae* and *S. pereirae.*—a. *Solanum oliveirae* (from *R. F. de Oliveira et al. 455* GUA). b, c. *Solanum pereirae* (from *E. Pereira 1270* RB).—b. Habit.—c. Portion of cymose-dichotomous flowering with straight rachis.

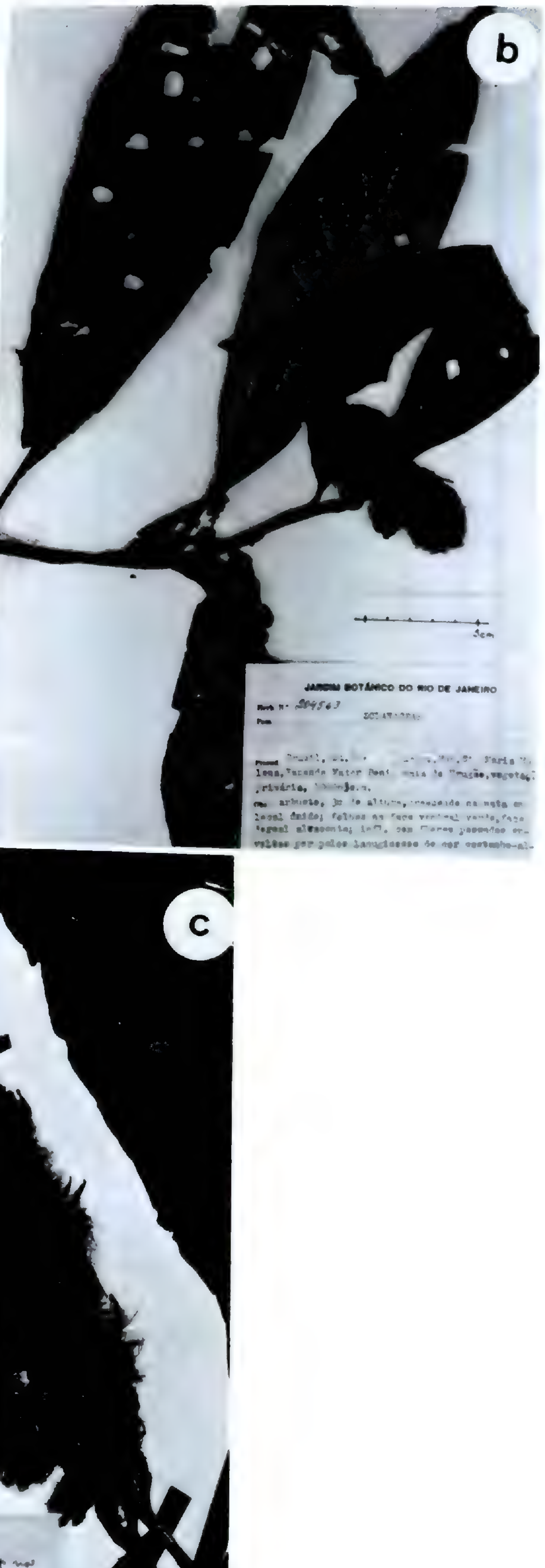

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FIGURE 17. *Solanum sooretamum* and *S. steyermarkii*. a, b. *Solanum sooretamum* (from *R. P. Belem 1534* US).—a. Habit with flowers.—b. Portion of cymose-dichotomous flowering with scorpioid rachis.—c. *Solanum steyermarkii* (from *J. A. Steyermark 35389* F). Fruiting branch.

Paratypes. BRAZIL. BAHIA: Municipality of Porto Seguro, km 19 on road to Vera Cruz and Vale Verde, 4 Apr. 1979 (fl, fr), *Mattos Silva et al. 349* (CEPEC, RB); Porto Seguro, Estação Ecológica Pau-Brasil, 4 Feb. 1972 (fl), *Eupunino 206* (CEPEC, NY); Santa Cruz Cabrália, 22 Mar. 1978 (fl), *Mori et al. 9823* (CEPEC); Conceição da Barra, 13 Nov. 1968, *Almeida 232* (CEPEC, RB). ESPÍRITO SANTO: Linhares, Reserva Florestal da Companhia Vale do Rio Doce, 17 Jan. 1975 (fl), *Peixoto et al. 406* (RB); Lagoa Central, 100–200 m, 30 Aug. 1973 (fl, fr), *Sucre et al. 10136* (RB). SÃO PAULO: Serra da Bocaina, Parque Nacional da Bocaina near River Jacu Pintado, 10 Feb. 1959 (fl, fr), *Pabst 4754* (HB); Ribeirão Rico, 28 July 1921, *Edwal 2568* (SP).

Distribution and habitat. *Solanum sooretamum* occurs in the state of Espírito Santo in the forest reserves of Sooretama and of Companhia Vale do Rio Doce, and also in the state of Bahia in the municipality of Porto Seguro in a forest known as "mata de Tabuleiro," which is still primary although disturbed enough to produce vigorous plants of this taxon. It also occurs in the state of São Paulo in the Parque Nacional de Bocaina.

Affinity. *Solanum sooretamum* is distinguished from *Solanum vellozianum* by the length of the inflorescence and by the lepidote-floccose indumentum with stellate long-pedicellate trichomes, which occurs on the abaxial surfaces of leaves and on branches. The geminate, globose sclerocytes are evident up into the apex of the fruit wall.

The epithet testifies to the plant's occurrence in the forest reserve of Sooretama.

10. Solanum steyermarkii Carvalho, sp. nov. TYPE: Guatemala. Dept. Quezaltenango: after volcano Santa Maria, between property Pirineos and Los Positos, 1,300–1,500 m, 8 Jan. 1940 (fl), *J. A. Steyermark 33825* (holotype, F). Figures 13, 17C.

Arbuscula ramis teretibus rigidis cum pedunculis, cymis, pedicelis, calyce et corolla extus adpresso-lepidotis argenteisque. Folia solitaria aut geminata in ramis novellis, falcata oblongo-lanceolate vel ovato-lanceolata apex longuiscule cuspidata, basi asymmetrica, margine integra vel leviter sinuata 50–180 mm longa et 20–75 mm lata, supra glabriuscula infra argentea, pilis peltato-stellatis cellulis radialibus ad tertiam partem connatis raro peltata. Flores parvi cymosi conferti pedicellati pubescentes oblongiquae. Cymae subopposititifoliae multiflorae subdichotomae erectae pedunculate. Bacca globosa glabriuscula, calyce non ampliato, ornata; seminis testa reticulata.

Trees 2–35 m tall and 5–10 m diam., branches terete, leafy, indumentum argenteous lepidote with peltate-stellate and rare peltate trichomes. Leaves solitary on young branches, membranaceous or nearly so, oblong-lanceolate to ovate-lanceolate, falcate, 5–18 cm long and 2–7 cm wide, apically reflexed, cuspidate to long-cuspidate, basally obtuse, slightly decurrent, slightly asymmetric, margin entire to sinuate; glabrescent above with sparsely peltate-stellate trichomes, densely lepidote beneath with peltate-stellate or rarely peltate trichomes 24–30 μm diam. having 15–19 radial cells, 9–12 μm long, the free portion 0.1–0.2 μm, at least ⅓ connected; 6–10 secondary veins prominent on the dorsal surface, camptodromous; petiole 0.4–1.3 cm long. Inflorescence subopposite the leaves, erect, 6–10 cm long, cymose-subdichotomous of about 50–100 flowers, rachis scorpioid, long-pedunculate, ca. 6 cm long. Flower buds oblong, 1–3 mm long; pedicels 3–4 mm long; calyx campanulate, 2 mm long, the lobes acute, to 1 mm long; corolla rotate-stellate, 4 mm long, the lobes acute, ca. 2 mm long; anthers ca. 1 mm long; ovary apically tomentose, the style curved. Berry globose, glabrescent, ca. 9 mm diam.; calyx persistent but not accrescent; seeds reniform with reticulate testa.

Paratypes. GUATEMALA. DEPT. SUCHITEPÉQUEZ: after Volcán Zunil, near property Las Nubes, 500–800 m, 2 Feb. 1940 (fr), *J. A. Steyermark 35389* (F). ALTA VERAPAZ: 210–250 m, between Hacienda Yaxcabnal along Río Icvolay and Río Apia, 13 Mar. 1942 (fr), *Steyermark 45027* (F). HUEHUETENANGO: between Ixcan and Río Ixcan, Cerro de los Cuchamatanes, 23 July 1942 *Steyermark 49220* (fr), (F). QUEZALTENANGO: near San Franscisco Miramar, Apr. 1905 (fl), *Pittier 72* (F); between Finca Pirineos and Patzulin, 1,200–1,400 m, 9 Feb. 1941 (fl), *Standley 86809* (F); between Santa Maria de Jesus and Calahuahe, 1,300–1,400 m, 5 Jan. 1940 (fl), *Steyermark 33504* (F). SAN MARCOS: Barranco Eminencia between San Marcos and San Rafael, 2,500–2,700 m, 6 Feb. 1961 (fl), *Standley 86234* (F). HONDURAS. Without other locality, 7 May 1934 (fl, fr), *Schipp 8-677* (F, S). MEXICO. CHIAPAS: June 1913, (fl) *Purpus 6958, 7010* (both F). PANAMA. BOCAS DEL TORO: Buena Vista, 1,500 m, 1 Mar. 1928 (fl, fr), *Cooper 620* (S); canal area, Barro Colorado Island, *Croat 11320* (MO), *Foster 1711* (MO); *Wetmore 200* (MO); Río Mendoza, *Nee 14031* (MO). COCLÉ: El Valle de Antón, Cerro Pilón, 2,000 m, 15 Aug. 1967 (fl), *Dwyer 7927, 7956* (both MO); 200–700 m (fl), *Dwyer 13955* (MO). DARIÉN: Cerro Tacarcuna, 1,500 m, 2 Feb. 1975, *Gentry 14107* (COL). PANAMA: Cerro Azul, 2,000 m, 17 July 1962, *Dwyer 2064* (MO); Goofy Lake, 1,800 m, 16 Aug. 1967 (fr), *Dwyer 8046* (COL, MO); El Llano, 25 July 1972 (fl), *D'Arcy et al. 6045* (MO); 26 Mar. 1975, *Dressler 4941* (MO). VENEZUELA. Colonia Tovar, 1854–1855, *Fendler 2609* (GOET, MO). COLOMBIA. CAUCA: Cordillera Central between Tacuejó and El Palo, 1,450–1,700 m, 21 Dec. 1944 (fl), *Cuatrecasas 19601* (F). CUNDINAMARCA: Mesistas del Colegio, Quebrada de Santa Marta, 1,240 m, 3 Mar. 1940, *Cuatrecasas 8225* (F). CHOCÓ: Alto de Limón, Río Sucio, 4 July 1976 (fr), *Forero et al. 1827* (COL, MO). HUILA: Quindío, 1,800 m, 1851–1857 (fl), *Triana* (BR, NY, P, W). VALLE: Cordillera Occidental between Marina and La Margarita,

4 Nov. 1944 (fl, fr), *Cuatrecasas* (F); Alto de Dinde between Cartago and Alaclá, 1,200–1,260 m, 16 Dec. 1946 (fl, fr), *Cuatrecasas 22886* (F). ECUADOR. LOS RÍOS: Sto. Domingo, *Dodson et al. s.n.* (fr) (MO). PERU. MADRE DE DIOS: near Manú, 10–11 Aug. 1974 (fl, fr), *Foster et al. 3210* (MO).

Distribution and habitat. This plant ranges from Guatemala to Peru and Venezuela at elevations from 500 to 2,700 m. Specimens have flowers and fruits in January and February.

Affinity. This species is similar to *Solanum lepidotum* but is distinguished by the indumentum always argenteous colored and constituted of peltate-stellate trichomes with radial cells, which are at least one-third connected, by the falcate, membranaceous leaves, and by the many-flowered, congested inflorescence.

The epithet is in homage to the late J. A. Steyermark, botanist at the Missouri Botanical Garden, a great connoisseur of the plant life of this region.

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ESPECIES NUEVAS Y COLECCIONES NOTABLES DE *DIOSCOREA* (DIOSCOREACEAE) EN MESOAMÉRICA[1]

Oswaldo Téllez Valdés[2] *y Bernice G. Schubert*[3]

Resumen

Se describen dos nuevas especies de *Dioscorea*, *D. carpomaculata* y *D. sumiderensis*, ambas de la región cubierta por la *Flora Mesoamericana*. Se presenta su distribución geográfica y ecológica así como notas acerca de su floración y fructificación. Se discuten las relaciones y la ubicación en secciones de cada especie. Se propone una nueva combinación basada en la información provista por colecciones recientes, y se presentan discusiones de especies notables.

Abstract

Two new species of *Dioscorea*, *D. carpomaculata* and *D. sumiderensis*, are described from the region encompassed by the *Flora Mesoamericana*. Geographical and ecological distributions and notes on flowering and fruiting are presented. Relationships and sectional placement are discussed for each species. Based on the information provided by recent collections, one new combination is made, and discussion and specimen citations of noteworthy species are provided.

A raiz del proyecto de la Flora Mesoamericana y el tratamiento de los grupos que la componen, colecciones botánicas sistemáticas e intensivas han sido realizadas, tanto en la región que cubre ésta flora, como en el resto de México. Estas colecciones proveen las bases de registros de taxa nuevos para México, así como para la ciencia, incluyendo las especies descritas en el presente trabajo.

Para cada una de las exsiccata se indica el sexo del especimen consultado, (♂) estaminado y (♀) pistilado.

Dioscorea carpomaculata O. Téllez & B. G. Schubert, sp. nov. TIPO: México. Chiapas: Mpio. Chiapa de Corzo, El Chorreadero, steep-walled canyon with tropical deciduous forest with *Hauya*, *Euphorbia*, *Diospyros*, *Cedrela*, *Trichilia*, and *Heliocarpus*, 800 m, 20 Aug. 1976, *D. E. Breedlove 39690* (holotipo, ENCB; isotipo, CAS). Figura 1.

Herbae scandentes glabrae. Caules sinistrorsum volubiles. Folia (3–)5.5–15.8 cm longa, (2–)4–15.5 cm lata, ovata vel suborbiculata, (7–)9–11 nervata. Inflorescentiae staminatae paniculatae 10–30 cm longae; flores 2–6 in cymis; stamina 6, distincta, basi tepalorum affixa, antheris introrsis; pistillodium conicum. Inflorescentiae pistillatae racemosae 15–30 cm longae. Capsulae 2.4–3.6 cm longae, 1.1–1.8 cm latae, maculato-laceratae; semina 10–15 mm longa, 7–9 mm lata, circumcirca alata.

Herbácea trepadora generalmente pubescente a glabra. Rizomas 0.3–1.0 m de largo, hipógeos,

[1] Derivado del proyecto de la Flora Mesoamericana, llevado a cabo entre el Instituto de Biología U.N.A.M. México, The Missouri Botanical Garden, U.S.A., y The Museum of Natural History, Great Britain. Agradecemos a CONACyT (PCECCNA-721259, 723355, 723357), a la D.G.A.P.A. al Jardín Botánico de Missouri en especial a, Enrique Forero y Gerrit Davidse, al Alfonso Delgado, Instituto de Biología U.N.A.M., al Herbario Gray y Arnold Arboretum, Universidad de Harvard, y a la Agencia para el Desarrollo Internacional (US-AID), por su apoyo económico para la consulta de herbarios. A los curadores de A, B, BM, C, CAS, EAP, ENCB, F, GH, HAL, K, LE, MEXU, MICH, MO, NY, P, TEFH, US, W, XAL las facilidades para la consulta de material. A Elvia Esparza, M. Rosa Martínez y Regina O. Hughes por las excelentes ilustraciones a las especies.

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napiformes, teretes, cónicos en el ápice, suculentos, corteza membranosa, pardo-amarillenta a color piel, internamente blancos, creciendo verticalmente. Tallos levovolubles, lineados, pubescentes a glabrescentes en la madurez. Hojas (3–)5.5–15.8 cm de largo, (2–)4–15.5 cm de ancho, alternas, ovadas a suborbiculares, base cordada, ápice cortiacuminado, haz esparcidamente estriguloso a glabrescente, envés generalmente densamente cinéreo-estrigoso a glabrescente, lámina con gran cantidad de rafidios visibles a trasluz; (7–)9–11-nervias, los nervios más exteriores generalmente bifurcados; pecíolos 6–10 cm de largo, ligeramente sulcados, puberulentos a glabrescentes. Inflorescencias estaminadas 1–4, racimos de cimas, de 10–30 cm de largo por axila; brácteas exteriores 1 mm de largo, ovado-lanceoladas, brácteas interiores 0.5–1 mm de largo, ovadas, ambas agudas, pilosas; flores 2–6 por cima, pedicelos 0.5–1 mm; perianto 2.5–3 mm, blanco o amarillento o crema, pubescente, los tépalos 2–3 mm de largo, oblongos a oblongo-lanceolados, patentes, ocasionalmente con puntuaciones glandulares translúcidas; estambres 6, ca. 1 mm, insertados en la base de los tépalos, anteras introrsas, tecas coherentes; pistilodio ca. 1 mm, cónico, ocasionalmente triacanalado. Inflorescencias pistiladas 1–4 racimos, de 15–30 cm por axila; brácteas similares a las estaminadas; flores solitarias, subsésiles; perianto 1–3 mm, blanquecino a pardo-amarillento, pubescente, los tépalos 1–3 mm, oblongos, patentes; estaminodios 6, ca. 0.7 mm, filiformes, insertados en la base de los tépalos; columna estilar ca. 1 mm, estilos bífidos, teretes, delgados. Cápsulas 2.4–3.6 cm de largo, 1.1–1.8 cm de ancho, oblongas a elípticas, base y ápice agudos, discoloras por una mácula longitudinal central pardo-oscura, con forma lacerada, las valvas densamente cinéreo-tomentosas cuando jóvenes a glabrescentes en la madurez, subleñosas; semillas 10–15 mm de largo, 7–9 mm de ancho, oblongas a elípticas, 2 por lóculo, aladas periféricamente, pardo-rojizas, lisas.

Material adicional examinado. MÉXICO. CHIHUAHUA: Guasaremos, Río Mayo, *Gentry 2328* ♂ (F). SINALOA: Mpio. de Culiacán, Las Tranquitas, 65 km al N de Culiacán, *Martínez et al. 4152* ♂ (MEXU). NAYARIT: Mpio. Santa María del Oro, 6 km al E de Santa María del Oro, *Téllez & Dávila 8991* ♂♀ (MEXU). GUERRERO: Mpio. de Acahuizotla, Agua de Obispo, *Zamudio s.n.* ♂, *Diego 2927* ♂ (FCUNAM, MEXU); Mpio. Guayameo, 7 km al S de la desviación a Placeres del Oro, Carr. Cd. Altamirano–Zihuatanejo, *Soto et al. 2308* ♂, *2313* ♀ (MEXU); El Viejo, 16 km al S de Río del Oro. Carr. Cd. Altamirano–Zihuatanejo, *Torres et al. 1269* ♀ (MEXU). MÉXICO: Peña de Organo, Tlatlaya, *Matuda 31109* ♂ (MEXU); Los Bejucos, Tejupilco, *Matuda 31383* ♂ (MEXU); Cerro de Ixtapan de la Sal, *Matuda 31710* (MEXU); Cañada de Nanchititla, Tejupilco, *Matuda 37456* ♂ (MEXU). OAXACA: Dist. Sola de Vega, El Vado, 1 km al W de San Sebastian, carr. Oaxaca–Puerto Escondido, *Torres et al. 431* ♂ (MEXU). CHIAPAS: Mpio. Amatenango, along the creek Chenek' ha' near Amatenango, *Shilom Ton 2681* ♀ (CAS, ENCB); Mpio. Arriaga, 6 km N of Arriaga, *Breedlove 27292* ♀ (MEXU); Mpio. Huixtla, 6–8 km NE of Huixtla road to Motozintla, *Breedlove 25963* ♂ (MEXU); Malpaso near Siltepec, *Matuda 4534* ♂ (F, GH, MEXU, NY); Mpio. Ixtapa, Zinacantan paraje of Muctajoc, *Laughlin 1589* ♀ (A); along Mexican highway 190 in the Zinacantan paraje of Muctajoc, *Breedlove 11874* ♀ (A, CAS); Mpio. Ocozocoautla, 18–20 km N of Ocozocoautla along road to Malpaso, *Breedlove 20989* ♀ (CAS, ENCB, MEXU, NY); Cerro El Ocote, 30 km NW of Ocozocoautla, *Breedlove 28929* (CAS, MEXU); 32 km N of Ocozocoautla camino a Malpaso, *Martínez 14337* ♀ (MEXU); Mpio. San Cristóbal Las Casas, km 1120, road Chiapa de Corzo–San Cristóbal Las Casas, *Schubert & Gómez-Pompa 1747* (MEXU); Mpio. Tonalá, Tonalá, *Guzmán 57* ♂ (ENCB); NW side Cerro Vernal, 25–30 km SE of Tonalá, *Breedlove 25635* ♂ (MEXU); Mpio. Trinitaria, Margaritas, Comitán, *Matuda 15784* ♂ (F); Mpio. Tuxtla, Colonia Grijalva, cerca de Tuxtla Gutiérrez, *Gómez-Pompa 139* ♂ (CAS, MEXU); El Sumidero, cafetal cerca de La Coyota, *Miranda 7912* (MEXU); along the road from El Bosque to Simojovel, *Shilom Ton 3090* ♀ (CAS, ENCB); Mpio. Unión Juárez, Finca Juárez, Escuintla, *Matuda 1776* ♂ (F, MEXU); Mpio. Venustiano Carranza, 3 mi. SW of Pinola Las Rosas, *Breedlove 11360* ♀ (A, ENCB); Esperanza, Escuintla, *Matuda 16543* ♂ (F, MEXU); Monte Cristo, *Matuda 15939* ♂ (F, MEXU); Mpio. Villa de Corzo, above El Chorreadero, *Breedlove 51559* ♀, *51567* ♂ (CAS); El Chorreadero, 5.6 mi. E of Chiapa de Corzo along Mexican Highway 190, *Laughlin 1129* ♂ (CAS); El Chorreadero, 5.6 mi. SE of Chiapa de Corzo, *Shilom Ton 2975* ♀ (CAS, ENCB); El Chorreadero Park, 6 mi. SE of Chiapa de Corzo, *Thorne 40190b* (CAS); Mpio. Villa Flores, Rancho Margarita, *Miranda 6417* ♂♀ (MEXU); Rancho Lindavista, 24 km E Villa Flores, *Miranda 6439* ♀ (MEXU). GUATEMALA. *Heyde & Lux 6391* ♂ (A, GH). ESCUINTLA: *Berlin 10* ♂ (MEXU, XAL), *20* (XAL). HUEHUETENANGO: Paso del Boquerón, along Río Trapichillo, below La Libertad, *Steyermark 51163* ♀ (F). EL SALVADOR. SONSONATE: *Calderón 1691* ♂ (GH).

Dioscorea carpomaculata representa un característico elemento de la sección *Macrogynodium* Uline del subgénero *Dioscorea*, cercanamente relacionado a *D. nelsonii* Uline. El material

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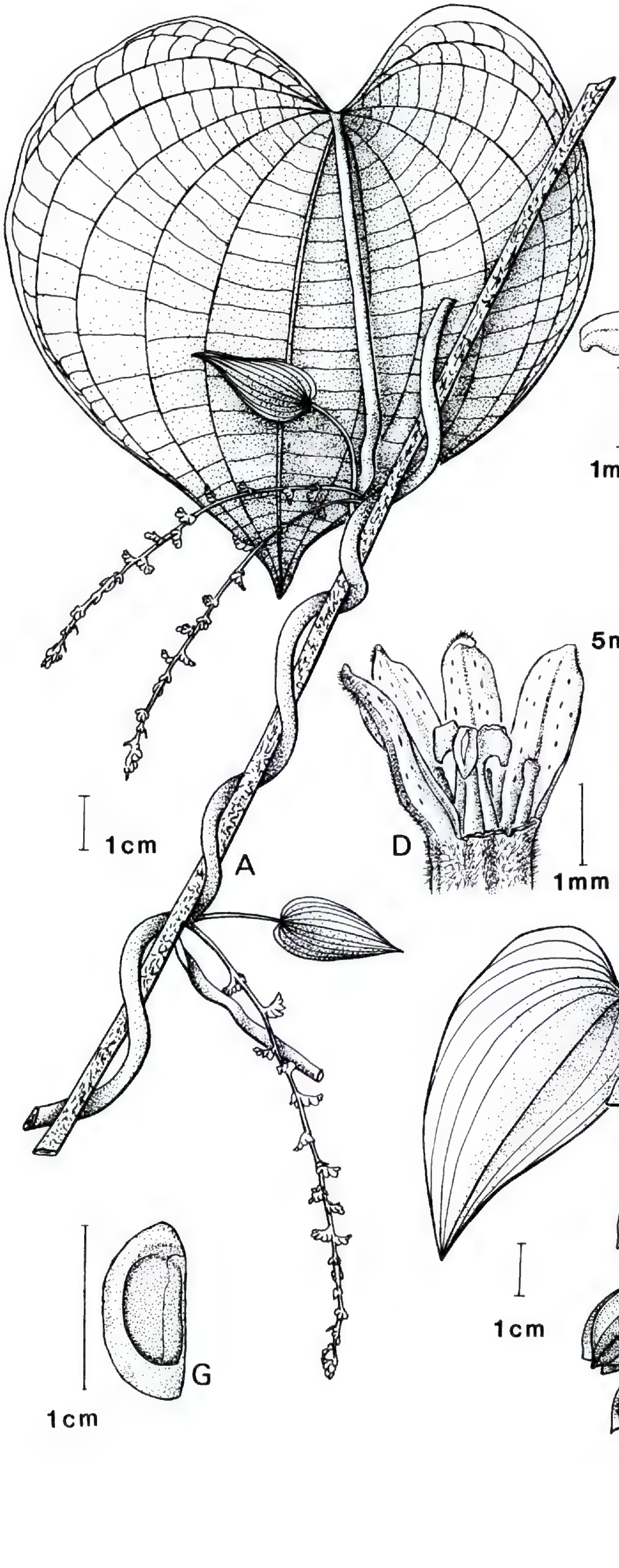
FIGURA 1. *Dioscorea carpomaculata* Téllez & Schubert.—A. Planta estaminada.—B. Planta pistilada con una infrutescencia.—C. Flor estaminada mostrando los 6 estambres y el pistilodio.—D. Flor pistilada mostrando los tépalos, estaminodios y la columna estilar.—E. Flor pistilada, ovario y brácteas.—F. Cápsula mostrando la mácula.—G. Semilla alada periféricamente. (A y C, *Breedlove 25635*; B, D–G, *Breedlove 39690*).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arriba citado ha sido frecuentemente confundido con *D. cymosula* Hemsl., especie erróneamente ubicada en la misma sección *Macrogynodium*; esta especie posee semillas aladas posteriormente, por lo que pertenece al subgénero *Helmia* (Kunth) Benth. En este trabajo se propone su reubicación en la sección *Chondrocarpa*. Ambas especies comparten un interesante número de caracteres, tanto de estructuras vegetativas como reproductivas, como ha sido mencionado por Burkill (1960), Téllez & Schubert (1987), y Medina et al. (en prep.) para algunas otras estructuras de numerosas especies de *Dioscorea*.

Dioscorea carpomaculata var. **cinerea** (Uline) O. Téllez & B. G. Schubert, comb. nov. *Dioscorea cymosula* Hemsl. var. *cinerea* Uline, Notizbl. Bot. Gart. Mus. Berlin-Dahlem 7: 202. 1917. TIPO: México. Oaxaca: *Knechtel 223* (B).

Esta variedad se caracteriza por su pubescencia tomentosa, principalmente sobre hojas y tallos jóvenes, y por las flores ligeramente más pilosas que en la var. *carpomaculata*. Habita principalmente en bosques mesófilos, por encima de los 1,500 m, y sólo se distribuye en Oaxaca y Chiapas.

Material examinado. MÉXICO. CHIAPAS: Mpio. Chiapa de Corzo, El Chorreadero State Park, 5.6 mi. SE of Chiapa de Corzo, *Thorne & Lathrop 40190a* (CAS); Mpio. de Huixtla, Honduras near Siltepec, *Matuda 4382* ♂ (GH, NY), *15957* ♂ (MEXU); Mpio. Jitotol, 6 mi. N of Jitotol, *Lathrop & Thorne 7333* (CAS); Mpio. of Soyalo, 5 km above Soyalo along road to Bochil, *Breedlove 10230* ♂ (CAS).

Dioscorea sumiderensis B. G. Schubert & O. Téllez, sp. nov. TIPO: México. Chiapas: Mpio. of La Trinitaria, 15 mi. S of Comitán along highway; mixed woodland and open grass slopes with limy rocks, ca. 2,000 ft., 20 Sep. 1952, *H.S. Gentry 12192* ♂♀ (holotipo, GH; isotipo, MEXU). Figura 2.

Herbae scandentes glabrae. Caules sinistrorsum volubiles. Caules, petioli et rhachides alati, dentato-serrulati. Folia (2.5–)4.5–8.8 cm longa, (2.1–)3.3–6.8 cm lata, ovata-cordata vel suborbiculata, 7–9 nervata. Inflorescentiae staminatae paniculatae 5–15 cm longae; flores 2–4(–5) in cymis; stamina 3, distincta, basi tepalorum affixa, antheris extrorsis; staminodia 3; pistillodium conicum. Inflorescentiae pistillatae racemosae 8–17 cm longae; staminodia 6, 3 longis, filiformibus, 3 brevibus, triangularibus, conicis. Capsulae 8–12.5 mm longae, (4–)6–10 mm latae, verrucosae; semina 4–7 mm longa, 3–5 mm lata, circumcirca alata.

Herbáceas trepadoras glabras. Rizomas de 5–15 cm de largo, de 1–1.5 cm de ancho, hipógeos, subteretes, con crecimiento longitudinal, corteza pardo-oscura, internamente blancos o cremas. Tallos levovolubles. Tallos, pecíolos y raquis de las inflorescencias conspicuamente alados, dentado-serrulados. Hojas de (2.5–)4.5–8.8 cm de largo, de (2.1–)3.3–6.8 cm de ancho, alternas, ovado-cordadas a suborbiculares, membranáceas, seno basal triangular a campanulado, base cordada, ápice agudo a estrechamente acuminado, 7–9-nervias, conspicuamente dentado-serruladas, las más exteriores generalmente bifurcadas; pecíolos de (0.8–)2.5–8 cm de largo. Inflorescencias estaminadas 1 a 3 racimos de glomérulos o fasciculos o 1–2 panículas compuestas, de 5–15 cm de largo por axila; brácteas exteriores de 1–2 mm de largo, de 0.5 mm de ancho, ovado-lanceoladas a lineal-lanceoladas, acuminadas, brácteas interiores de ca. 1 mm de largo, de 0.4 mm de ancho, ovadas, acuminadas; flores 2–4(–5) por cima, pedicelos 1–2 mm; perianto de 1–2 mm, verdoso o amarillento o crema, los tépalos de 1–2 mm de largo, de 0.5–0.7 mm de ancho, ovales, ovados o cortamente oblongos u oblongo-lanceolados; estambres 3, de ca. 0.8 mm de largo, insertados en la base de los tépalos, las anteras extrorsas, las tecas coherentes, estaminodios 3, de 0.5–0.6 mm de largo, ligeramente geniculados o curvados casi en ángulo recto, con una pequeña prolongación surgiendo en la curvatura cerca de la parte media del estaminodio, espatuláceos y verrugosos en el tercio apical, insertados en la base de los tépalos; pistilodio de 0.1–0.2 mm de alto, cónico o trilobado. Inflorescencias pistiladas un racimo, de 8–17 cm de largo por axila; brácteas exteriores de 1–2 mm de largo, de 0.5 mm de ancho, ovado-lanceoladas, acuminadas, brácteas interiores de ca. 1 mm de largo, de 0.4 mm de ancho, ovadas, acuminadas; flores solitarias, subsésiles; perianto de 1–2 mm, verdoso o amarillento o crema, los tépalos de 1–2 mm de largo, de 0.5–0.7 mm de ancho, ovales, ovados a cortamente

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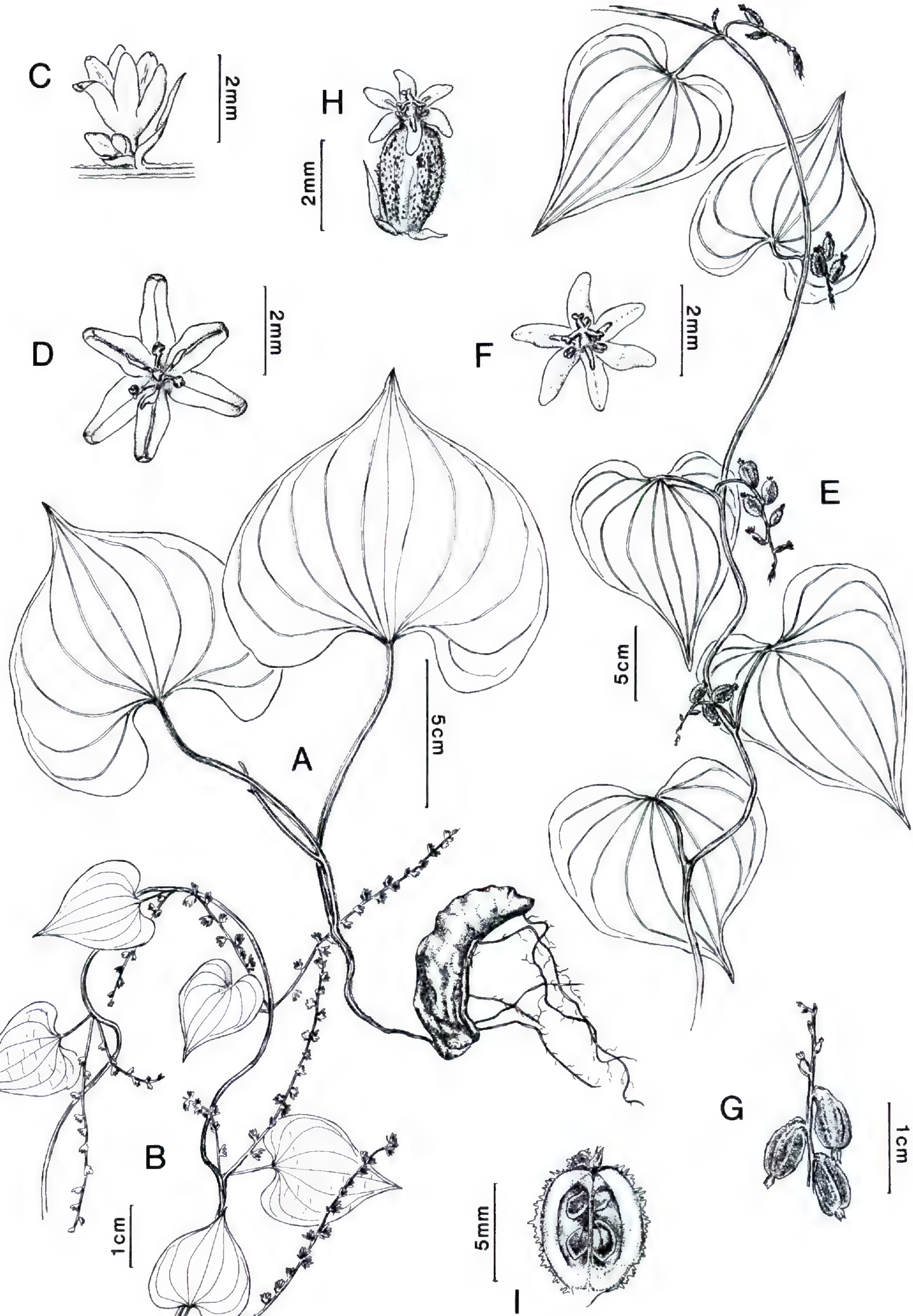
FIGURA 2. *Dioscorea sumiderensis* Schubert & Téllez.—A. Planta jóven con rizoma, mostrando tallos y pecíolos alados, ×1.—B. Planta estaminada con inflorescencia, ×2.—C. Flores estaminadas y botones florales, ×15.—D. Flor estaminada abierta mostrando 3 estambres y 3 estaminodios, ×15.—E. Planta pistilada con infrutescencia jóven, ×2.—F. Flor pistilada abierta mostrando los 6 estaminodios y la columna estilar, ×15.—G. Infrutescencia, ×3.—H. Fruto jóven, ×15.—I. Corte longitudinal de la cápsula, mostrando los 2 lóculos y las semillas en cada uno, ×6. (A–D, *H. S. Gentry 12191*; E–I, *H. S. Gentry 12192*).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5mm

oblongos u oblongo-lanceolados; estaminodios 6, 3 largos de 0.4–0.5 mm de largo, filiformes, 3 cortos de ca. 0.2 mm de largo, cónicos, triangulares o piramidales, insertados en la base de los tépalos; los estilos 3, unidos en una columna estilar de ca. 1 mm de alto, bífidos, delgados, teretes, los estigmas 6. Cápsulas 8–12.5 mm de largo, de (4–)6–10 mm de ancho, oblongas a obovadas, ligeramente más amplias arriba del tercio basal, verrugosas; semillas 4–7 mm de largo, de 3–5 mm de ancho, oblongas a suborbiculares, 2 por lóculo, aladas periféricamente, pardo-rojizas, lisas.

Material adicional examinado. MÉXICO. CHIAPAS: Mpio. Berriozabal, 5 km E of Berriozabal, *Breedlove 20405* ♀ (CAS); Mpio. Mazapa, Río Motozintla between Amatenango de la Frontera and Mazapa, *Breedlove & Strother 46149* ♀ (CAS); Mpio. La Trinitaria, 11 mi. S of La Trinitaria, *Breedlove & Raven 13243* ♂♀ (CAS); 15 mi. S of Comitán along highway, *H.S.Gentry 12191* ♂ (GH, MEXU); Mpio. Tuxtla Gutiérrez, Camino Sumidero-Tuxtla Gutiérrez, *Cid Rojas CR160* ♀, *CR161* ♀, *CR162* ♀, *CR163* ♀, *CR165* ♀ (XAL); Sumidero, *Cox & González 1856* ♀ (XAL), *1857* ♂ (MEXU), *1858* ♂ (XAL); Mpio. Venustiano Carranza, Soyatitán, from Las Rosas to Pugiltik, *Shilom Ton 3128a* ♀, *3142* ♂ (CAS, ENCB); Mpio. Villa de Corzo, road to Nueva Concordia, *Breedlove 37596* ♂ (CAS); Mpio. Villa Flores, Cuchulote–Magdalena–Villaflores, Robledal, *Cid Rojas CR169* ♀ (XAL).

Especie cercanamente relacionada a *Dioscorea matagalpensis* en la sección *Lychnostemon*, ambas poseen estaminodios más cortos que los estambres, curvados casi en ángulo recto con una ligera prolongación surgiendo perpendicularmente en la parte media del estaminodio, así como periantos pequeños, agrupados en cimas muy cortas. Sin embargo, se diferencian por la presencia del ala dentado-serrulada en tallos, pecíolos y raquis, y los frutos verrugosos en *D. sumiderensis*, contra las mismas estructuras todas lisas en *D. matagalpensis*, con excepción del raquis de la inflorescencia ligeramente dentado-serrulado.

En el proyecto Flora Mesoamericana, se han realizado colecciones notables de material de algunas especies problemáticas. Numerosas especies de *Dioscorea* han sido descritas de uno de los sexos, situación que ha causado muchos problemas, el más común de ellos siendo la descripción de la misma especie en dos ocasiones, una basada en el estaminado y otra en el pistilado. A continuación se brindan discusiones acerca de algunas de éstas especies y el material de referencia consultado.

Dioscorea chiapasensis Matuda, Bol. Soc. Bot. México 15: 25. 1953. TIPO: México. Chiapas: En matorral claro, Unión Juárez, falda sur del Volcán Tacaná, alt. 1,400 m, 17 marzo 1939, *Matuda 2781* ♂ (holotipo, MEXU; isotipos, F, GH, NA, US).

Dioscorea chiapasensis es claramente un elemento de la sección *Apodostemon*, ya que presenta los 6 estambres cási sésiles, el pistilodio cónico a triangular, las semillas aladas periféricamente y el polen estriado. Sin embargo, su fruto es el más pequeño de la sección, entre 8–12 × 5–7 mm, y difiere considerablemente de los característicos de esta sección anotada, ya que es oblongo-elíptico, con la base y el ápice agudos, a diferencia del resto de las especies que presentan frutos con el ápice redondeado a truncado, y con forma oblanceolada a subcuadrada o elíptico hasta redondeado.

Esta especie habita principalmente en bosques de *Pinus* y bosques mesófilos de montaña entre los 1,000–1,700 m, siendo endémica del sur de México y Guatemala.

Material adicional examinado. MÉXICO. CHIAPAS: Mpio. Unión Juárez, Volcán Tacaná a 500 m al E de Talquian, *Martínez & Reyes 20333* ♂♀, *20334* ♂ (MEXU). GUATEMALA. QUEZALTENANGO: Finca Pirineos, below Santa María de Jesús, *Standley 68278* ♂, *68395* ♂ (F). RETALHULEU: Sierra Siete Orejas, 20 km N of San Sebastián, *Gentry 12546* ♂, *12566* ♂♀ (GH, NA). SAN MARCOS: Río Mopa, below Rodeo, *Standley 68786* ♂ (F). SOLOLÁ: Río Bravo in vicinity of Finca Moca, S slope Volcán Atitlán, *Steyermark 47960* ♀ (F, NA).

Dioscorea cyanisticta J. D. Smith, Bot. Gaz. (Crawfordsville) 20: 10. 1895. TIPO: Costa Rica. Cartago: Río Turrialba, *Donnell-Smith 4969* ♂ (holotipo, US; isotipos, F, GH).

Dioscorea cyanisticta, de la sección *Brachystigma*, está cercanamente relacionada a *D. densiflora* de la sección *Oxypetalum*, (no obstante pertenecen a diferentes secciones). Se caracteriza por sus estaminodios espatuláceos, más largos que los estambres y muy similares a los de *D. densiflora*. Por otra parte, sus frutos son más grandes que en *D. densiflora*, suculentos, y producen gran cantidad de líquido mucilaginoso mientras maduran, y generalmente son glaucos. Ocasionalmente producen tres semillas por lóculo en vez de las dos normalmente encontradas en la mayoría de las especies de *Dioscorea*.

Material adicional examinado. MÉXICO. CHIAPAS: Mpio. de Bochil, along river E of Bochil, *Shilom Ton 4005* ♂ (CAS, ENCB); Mpio. de Jitotol, 5 mi. S of Jitotol, *Breedlove 11936* ♂ (CAS, ENCB, GH); km 18 Col. Cuauhtémoc, *Shilom Ton 8154* (MEXU); Mpio. Huixtla, Escuintla, *Matuda 1018* ♂ (GH); Pinabeto, Motozintla, *Matuda 15482* ♂ (F); Mpio. La Trinitaria, km 18 Col. Cuauhtémoc, *Shilom Ton 8154* ♂, *8211* ♂, *8869* ♂ (MEXU); 10 km ENE of Dos Lagos above Santa Elena,

Breedlove 58413 ♂ (ENCB, MEXU); Mpio. Unión Juárez, Volcán Tacaná, Talquian, *Téllez & Martínez 8939* ♂♀, *8945* ♀ (MEXU), *42546* ♂ (MEXU); Volcán Tacaná, 500 m al E de Talquian, *Martínez & Reyes 20331* (MEXU); Volcán Tacaná, Chiquihuite, *Matuda 2817* ♂ (F, NA); Ejido Eureka, *Syntex JP1272* ♂ (MEXU). GUATEMALA. ALTA VERAPAZ: Región del Chicoj, NE of Carchá, *Standley 70032* ♂ (F). QUEZALTENANGO: Finca Azucena, above Colomba, *Standley 68090* ♂ (F); above Mujuhá, entre San Martín Chile Verde y Colomba, *Standley 85481* ♂ (F). SAN MARCOS: above Finca El Porvenir on Todos Santos Chiquitos, *Steyermark 37165* ♂ (F). ZACAPA: slopes of Monte Virgen, *Steyermark 42456* ♂♀ (F). NICARAGUA. MADRIZ: Cerro Volcán Somoto, *Moreno 20023a* ♂, *20068* ♀ (MO), *Stevens & Grijalva 16411* (MO); Cerro Quiusca, *Stevens & Grijalva 16130b* (MO). MATAGALPA: Macizos Peñas Blancas, *Stevens et al. 21103* ♂ (GH, MO). COSTA RICA. GUANACASTE: Santa Elena to Tilarán road, *Khan et al. 1131* ♂ (BM). ALAJUELA: Reserva Forestal San Lorenzo, *Carvajal 164* ♂ (MEXU, MO).

Dioscorea koepperi Standley, Field Mus. Nat. Hist. 9: 269–270. 1940. TIPO: Honduras. Atlántida near Río Danto, lower slope of Mt. Cangrejal, near La Ceiba, 16 July 1938, *Yuncker, Koepper & Wagner 8482* ♂ (holotipo, F; isotipos, GH, P, US).

Dioscorea koepperi presenta una serie de caracteres que le ubican claramente en la sección *Apodostemon*, tales como la presencia de seis estambres casi sésiles insertados en el toro, pistilodio cónico, tripartido, seis estaminodios cónicos y pequeños, estilos amplios carnosos, festoneados o umbraculados y unidos en una corta columna, así como semillas aladas periféricamente. Se encuentra cercanamente relacionada a *D. pumicicola* ya que comparten importantes caracteres como son, los rizomas esféricos con fuertes adelgazamientos intermedios entre los cuerpos principales (como probable estrategia de reproducción vegetativa), la forma semejante de las hojas, y la forma y color de los frutos. Representa a su vez una interesante vicarianza, ya que *D. koepperi* as endémica de Honduras, en una sola localidad en la vertiente Atlántica, en el Monte Cangrejal, entre 0–50 msnm, habitando la selva alta perennifolia. *Dioscorea pumicicola* se encuentra solamente en el estado de Morelos, México, en una región muy reducida, habitando la selva baja caducifolia, alrededor de 800 msnm.

Material adicional examinado. HONDURAS. ATLÁNTIDA: 5 km al S de Danto, en las represas del SANAA (Sistema de Aguas y Alcantarillados) sobre el Río Danto, por el camino que sale atrás del poblado, selva alta perennifolia, 10 junio 1985, *Téllez & Martínez 8848* ♂♀ (topotipo, MEXU).

Dioscorea lepida C. V. Morton, Carnegie Inst. Wash. Publ. 461: 248. 1936. TIPO: Costa Rica. Provincia de San José, Laguna de la Chonta, NE of Santa María de Dota, alt. 2,000–2,100 m, 18 Dec. 1925, *Standley 42133* (holotipo, US; isotipo, NY).

D. racemosa (Klotzsch) Uline var. *hoffmannii* Uline in Engler's Bot. Jahrb. 22: 431. 1897. TIPO: Costa Rica. Candelaria, *Hoffmann 614* ♂♀ (holotipo, B).

Dioscorea lepida fue ubicada erróneamente en la sección *Trigonobasis* por Morton (1936) quien anota "easily distinguished from other species of the section *Trigonobasis* by the small, acute, readily dehiscent capsules." Sin embargo, estas características son compartidas por numerosas especies en el subgénero *Helmia*. Esta especie se excluye fácilmente por poseer estambres en una columna, extrorsos y los estilos en una columna, a diferencia de los estambres libres, introrsos y los estilos también libres en la sección *Trigonobasis*. Por las características anotadas, esta especie debe permanecer conjuntamente con *D. standleyi* en la sección *Arestophyton* (ver discusión en *D. standleyi*).

Dioscorea lepida tiene un comportamiento reproductivo particular. En primer término, cuando las semillas son dispersadas, éstas ocupan muy frecuentemente las horquetas superiores de los árboles principales y más altos del dosel, donde germinan y desarrollan hasta formar pequeños, pero fuertes rizomas epífitos, al igual que *D. standleyi*. Por otra parte, aparentemente dependiendo de las condiciones del medio, su comportamiento "sexual" es particular. Esta especie ha sido colectada en espécimen pistilado con todo y su rizoma, y este mismo rizoma ha producido especímenes estaminados o monoicos alternativamente, a través de varios años entre 1983–1988; *Téllez 8212* ♂, *9357* monoica (MEXU).

Dioscorea lepida también presenta un interesante patrón de distribución discontínua a través de Mesoamérica, en áreas que se relacionan con las denominadas "zonas refugio" en partes de Centroamérica y el sur de México. Se ha definido así, ya que la distribución de esta especie encaja perfectamente en varios casos en los patrones de zonas con características de refugios, dados por Haffer (1982), Prance (1982), Toledo (1982), y Wendt (1989), quienes señalan que son zonas de gran precipitación y humedad y alta diversidad biológica, predominando tipos de vegetación como la selva alta perennifolia o el bosque mesófilo de mon-

taña. En algunos casos, *D. lepida* se encontró en las mismas zonas que estos autores determinaron como probables refugios y en otros casos habitando zonas con características similares a las de estos refugios. Su distribución geográfica es del sur de México, de Chiapas hasta Panamá en Centroamérica. Habita en la selva tropical húmeda y los bosques mesófilos y de neblina, entre los 350–2,010 m. Florece y fructifica de julio a marzo.

Material adicional examinado. MEXICO. CHIAPAS. Mpio. Berriozabal, 13 km N of Berriozabal near Pozo Turipache and Finca El Suspiro, *Breedlove 20247* ♂ (CAS, ENCB, MO); *Téllez et al. 7605* ♀ (GH, MEXU); Mpio. la Trinitaria, 15 km ENE of Dos Lagos above Santa Elena, *Breedlove 56660* ♂♀ (CAS); 10 km ENE of Dos Lagos above Santa Elena, *Breedlove 57560* ♂♀ (CAS). GUATEMALA. ALTA VERAPAZ: Quebradas Secas, *Johnson 869* ♂♀ (US). CHIQUIMULA: Cerro Tixixi (Tishishi), 3–5 mi. N of Jocotán, *Steyermark 31622* ♂ (GH). IZABAL: Cerro San Gil, *Steyermark 41955* ♀ (F). HONDURAS. COMAYAGUA: Cerro Azul de Meambar, *Hazlett 1853* ♂ (TEFH). COSTA RICA. ALAJUELA: Reserva Forestal San Ramón, *Carvajal 356* ♀ (MEXU, MO); Zarcero, Cantón Alfaro Ruiz, *Smith H1353* ♀ (GH). CARTAGO: 1.5 km SW of Tapantí, along Río Grande de Orosí, *Lent 1813* ♂♀ (F); 8 km S of Tapantí, *Lent 1229* ♂ (F); Finca El Chaparral, 4.5 km S of bridge on Agua Caliente at Lourdes, *Liesner & Judziewicz 14621* ♂♀ (MO). GUANACASTE–ALAJUELA: Miravalles above Bijagua, *Gómez et al. 19116* ♂ (MEXU, MO). PUNTARENAS: Upper Río Burú, *Gómez et al. 21518* ♂, *21756* (MEXU, MO). SAN JOSÉ: trailside above Río Honduras, *Lent 2261* ♂♀ (F); vicinity of El General, *Skutch 3021* ♀ (GH); La Palma de San Ramón, *Brenes 5124* ♂♀ (F); 3 mi. NE of El Copey, *Stork 1629* ♂ (F). PANAMA. CHIRIQUÍ: Cerro Colorado, 20–28 mi. from San Felix, *Croat 33354* ♂♀ (GH). COCLÉ: 1.5 mi. from El Copé, *Croat 44553* ♀ (MEXU, MO); El Valle de Antón, La Mesa above El Valle, *Nevers et al. 6337* (MO). LOS SANTOS Y VERAGUAS: 10 km SW of El Cortezo (Prov. Los Santos), *Hammel 5380* ♂ (MO). PANAMÁ: top of Cerro Campana, *D'Arcy 15086* ♂ (MEXU, MO); Cerro Campana along trail to summit, *Miller & Miller 981* ♂ (MEXU, MO), *Madison 777* ♀ (GH); Cerro Campana, *Smith & Smith 3364* ♂♀ (A, US); *Stein & Hamilton 1137* ♀, *1160* ♂ (MEXU, MO); El Llano-Cartí road, 6.8 miles from the highway, *Croat 49131* ♀ (MO); El Llano to Carti–Tulipé road, *Kennedy 2711* ♀ (NY). VERAGUAS: along road between Santa Fé and Escuela Agrícola Alto Piedra, *Croat 26005* ♀ (MO); Rancho Chorro mountain above Torti Arriba, *Folsom et al. s.n.* ♂♀ (MO); 6–7 km W of Sta. Fe, *Nee 9784* (TEFH).

Dioscorea standleyi C. V. Morton, Carnegie Inst. Wash. Publ. 461: 252–253. 1936. TIPO: Costa Rica. Provincia San José: in wet forest at La Hondura, alt. 1,200–1,500 m, 9 Mar. 1929, *P. C. Standley & J. Valerio 51877* ♀ (holotipo, US).

Esta especie se ubica erróneamente en la nueva sección *Arestophyton*, en el subgénero *Dioscorea*, no obstante haber sido descrito con base en material pistilado por Morton (1936). Sin embargo, muchas colecciones recientes demuestran que esta especie posee semillas aladas solamente en su parte posterior, caracter que la ubica en el subgénero *Helmia*.

Esta especie habita primordialmente los bosques húmedos de neblina, mesófilo y pluvial premontano, entre los 300–2,040 m. Florece y fructifica prácticamente durante todo el año.

Material adicional examinado. COSTA RICA. ALAJUELA: Reserva Forestal San Ramón, *Carvajal 356* ♀ (MEXU, MO); Virgen del Socorro, *Chacón y Herrera 1187* ♀ (MEXU, MO); *Solomon 2473* ♂ (GH); Vara Blanca de Sarapiquí, between Poás and Barba volcanoes, *Skutch 3562, 3623* ♂ (GH); La Peña, Cantón Alfaro Ruiz, *Smith p-2168* ♂ (GH); San Ramón northward Balsa, ca. 16.7 km N of bridge over Quebrada Volio, *Stevens 13891* ♂ (MO); ca. 13.8 km N of bridge over Quebrada Volio, *Stevens 13747* ♂ (MO); 5.7 km N of bridge over Quebrada Volio, *Stevens 14099* ♂ (MO); 15 km NNW of San Ramón, *Liesner & Judziewicz 14845* ♀ (MO). CARTAGO: 12 km S of Turrialba, *Liesner 14337* ♂ (MEXU, MO). HEREDIA: 4 mi. N of Vara Blanca, *Croat 35569* ♂ (GH); 3 mi. S of Cariblanco, *Croat 35809* ♂ (GH); La Palma, Braulio Carrillo National Park, *Garwood et al. 366* ♂ (BM, MEXU); road between San Rafael and Río las Vueltas, *Stevens 13928* ♂ (MO). PUNTARENAS: just N of Sta. Elena on Fila Coton, S of Agua Caliente, *Davidse et al. 28284* ♂ (MEXU, MO). PANAMÁ. CHIRIQUÍ: camino hacia La Soledad, *Correa et al. 2061* (GH); Quebrada Bonito, *D'Arcy et al. 15887* (MEXU, MO), *Churchill 5749* ♂ (MO); Fortuna Dam area, between Quebrada Los Chorros and Quebrada Hondo, *Churchill y Churchill 6084* ♂ (MO); Cerro Colorado, *Folson et al. 4727* ♂ (MEXU, MO); Bocas del Toro, *McPherson 7223* ♂ (MEXU, MO); Fortuna dam site, above Gualaco, *Croat 49966* ♂, *50057* ♂ (GH), *McPherson 6680* ♂ (MEXU, MO); along Quebrada de Arena, *McPherson 7771* ♂ (MEXU, MO); Distr. Bugaba, Santa Clara to Cerro Pando, *V. der Werff y Herrera 7216* ♂ (MEXU, MO), Cerro Punta, *V. der Werff y Herrera 6470* ♀ (MEXU, MO); vicinity of Bajo Chorro, *Woodson y Schery 652* ♂, *664* ♂ (GH).

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NOTES

NEW COMBINATIONS AND A NEW VARIETY IN THE CYPERACEAE OF MESOAMERICA

Studies of sedges for *Flora Mesoamericana* have resulted in the following innovations.

Cyperus manimae Kunth var. **apiculatus** (Liebm.) C. Adams, comb. et stat. nov. *C. apiculatus* Liebm., Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Afh., ser. 5, 2: 220. 1850. TYPE: Mexico: S. Antonio Huatusco, *Liebmann 14352* (holotype, C).

Diplacrum mitracarpoides (Standley & L. O. Williams) C. Adams, comb. nov. *Scleria mitracarpoides* Standley & L. O. Williams, Ceiba 3: 36. 1952. TYPE: Honduras. El Paraíso: abundant in a wet season bog in a savanna near El Limonal, 650 m, 31 Dec. 1950, *Louis O. Williams 17323* (holotype, EAP; isotypes, BM, F, MO).

Pycreus flavicomus (Michaux) C. Adams, comb. nov. *Cyperus flavicomus* Michaux, Fl. Bor.-Amer. 1: 27. 1803. TYPE: United States: "Carolina."

Pycreus fugax (Liebm.) C. Adams, comb. nov. *Cyperus fugax* Liebm., Kongel. Danske Vidensk. Selsk. Naturvidensk. Math. Afh., ser. 5, 2: 196. 1850. TYPE: Mexico: Chinanthla, *Liebmann s.n.* (isotype, K).

Scirpus analecti Beetle, Brittonia 5: 148, 1944, var. **evadens** C. Adams, var. nov. TYPE: Mexico. Chiapas: steep slope with *Quercus* and *Pinus*, 3 mi. south of Aguacatenango along road to Pinola Las Rosas, Municipio of Venustiano Carranza, 5,600 ft., 25 June 1965, *Breedlove 10570* (holotype, F-1679132).

Ab inflorescentia spiculis omnino remotis non fasciculatis, et pedicelli usque ad 2(–5) cm longi, a *S. analecto* distinguendus.

Distinguished from *Scirpus analecti* by inflorescence with all spikelets well separated, not clustered, and pedicels to 2(–5) cm long. Typical *S. analecti* has the spikelets borne on pedicels less than 1 cm long.

Torulinium macrocephalum (Liebm.) C. B. Clarke, Kew Bull., Add. Ser. 8: 20. 1908, var. **eggersii** (Boeckeler) C. Adams, comb. et stat. nov. *Cyperus eggersii* Boeckeler, Beitr. Cyper. 1: 53. 1888. TYPE: Dominican Republic: Santo Domingo, near Batey, Río Yasica, 23 June 1887, *Eggers 2627* (holotype, B).

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A NEW BRAZILIAN SPECIES OF *DALECHAMPIA* SUBSECT. *TRIPHYLLAE* (EUPHORBIACEAE)

Dalechampia allemii is described as a new species in sect. *Dalechampia* subsect. *Triphyllae*. This new species from Bahia, Brazil, is isolated within subsect. *Triphyllae* because of its unguiculate involucral bracts, suppressed adstaminate pistillate bractlets, and sparsely lobed pistillate sepals. A key is provided to the Brazilian species of subsect. *Triphyllae*.

During a field trip to Brazil in 1978 with Antonio Allem of EMBRAPA/CENARGEN, Brasilia, I encountered an interesting species of *Dalechampia* in the scrubby vegetation in the interior of the state of Bahia. This plant clearly has not been described, and indeed does not appear to have any very close relatives.

Dalechampia allemii Webster, sp. nov., sect. *Dalechampia* subsect. *Triphyllae*. TYPE: Brazil. Bahia: Mun. Andaraí, scrub at edge of forest, 50 km NW of Andaraí, 15 Nov. 1984, *A. C. Allem, G. L. Webster & W. L. Werneck 2980* (holotype, CEN; isotype, DAV). Figure 1.

Habitu *D. clausseniana* et *D. olfersiana* similis, sed differt bracteis involucratis unguiculatis, involucello subtrifido, sepalis ♀ lobis paucis.

Twining vine; flowering stems terete, puberulent near tips with retrorsely recurved hairs 0.1–0.2 mm long and sparse, spreading hairs 0.3–0.5 mm long. Leaves: stipules reflexed, deciduous, lanceolate, strigose (hairs mostly 0.3–0.6 mm long), 3–3.5 × 0.7–1 mm; petiole puberulent as the stems, 2.5–5 cm long; stipels at base of blade lanceolate, 0.8–1.7 mm long; lamina chartaceous, 3-foliolate, sparsely hirtellous on veins and margins; middle leaflet elliptic-lanceolate, apiculate or shortly acuminate at the tip, pinnately veined (major laterals 5 or 6 on a side), 4.5–6.5 × 1.7–4 cm; lateral leaflets asymmetrically elliptic, apiculate, with 2 veins from base, 3–4 × 1.5–2.2 cm; veinlets somewhat prominulous beneath; margins entire. Inflorescences solitary on axillary shoots 0.3–0.7 cm long, with a single reduced or obsolete leaf (blade < 0.5 cm long) at the single node; peduncle becoming 1.8–2.5 cm long; involucral bracts pale yellowish green at anthesis, 1–1.3 × 0.7–1 cm, distinctly unguiculate (claw about ½ length of bract), deeply 3-lobed; lobes entire, with stimulose and simple hairs proximally; middle lobe elliptic-lanceolate, 0.6–1 × 0.15–2 cm; lateral lobes somewhat falcate, 0.5–0.7 × 0.2–0.3 cm; bracteal stipules lanceolate, slightly unequal, 1.8–2.2 × 0.9–1.2 mm. Pistillate cymule: abstaminate bract ovate, eglandular, 1.2–2.2 × 2 mm; adstaminate bractlets suppressed. Pistillate flowers subsessile or with pedicels up to 1.5 mm at anthesis; sepals generally 6, usually with 1 or 2 lateral lobes below the middle, sometimes with minute intercalary sepaloid projections; lobes minutely apiculate but not glandular-capitate; ovary minutely hispidulous; stylar column cylindrical, glabrous or sparsely hispidulous below, ca. 5 × 0.5 mm, with stigmatic bands extending ⅔ the length; stylar apex excavated, eccentric, 0.4–0.6 × 0.6–0.8 mm. Staminate cymule with densely hispidulous peduncle up to ca. 2 mm long; involucel 2-lipped, rather deeply 4-lobed (but middle adpistillate lobe reduced or suppressed); lateral adpistillate lobes ovate, 2.5–5 × 3.5–7 mm, margins entire or sometimes remotely and minutely glandular; adpistillate central lobe elliptic, small (1–1.5 mm long) or obsolete; abpistillate lobe 1.5–2.5 × 3 mm, enclosing the resiniferous gland; gland ca. 2 × 3.5 mm, of 1 or 2 rows of entire laminar ceriferous bractlets; resinous secretion pale, whitish. Staminate flowers subsessile; mature buds angled, 2.3–2.8 mm across, glabrous or nearly so; calyx splitting into 3 or 4 recurving segments 1.8–2.5 × 1.3–1.8 mm; staminal column very short (0.5 mm or less), glabrous; stamens 50–80; filaments glabrous, 0.2–0.3 mm long; anthers ca. 0.4 mm long. Middle fruiting pedicel 8–10 mm long, lateral fruiting pedicels 2.5–4 mm long; fruiting sepals 3–4 × 0.4–0.8 mm, flattened, mostly with a pair of medial lateral lobes ca. 0.2–0.5 mm long; columella ca. 4 mm long; capsule valves ca. 5.5 mm long, inconspicuously strigose-hispidulous; seeds not seen.

Additional specimens examined. BRAZIL. BAHIA: Mun. Andaraí, Km 39, Andaraí, BR 242, 4 Mar. 1978, *Allem & Vieira 1801, 1802* (CEN, DAV).

Dalechampia allemii appears outstanding among all known species of sect. *Dalechampia* subsect. *Triphyllae* (Webster & Armbruster, 1990)

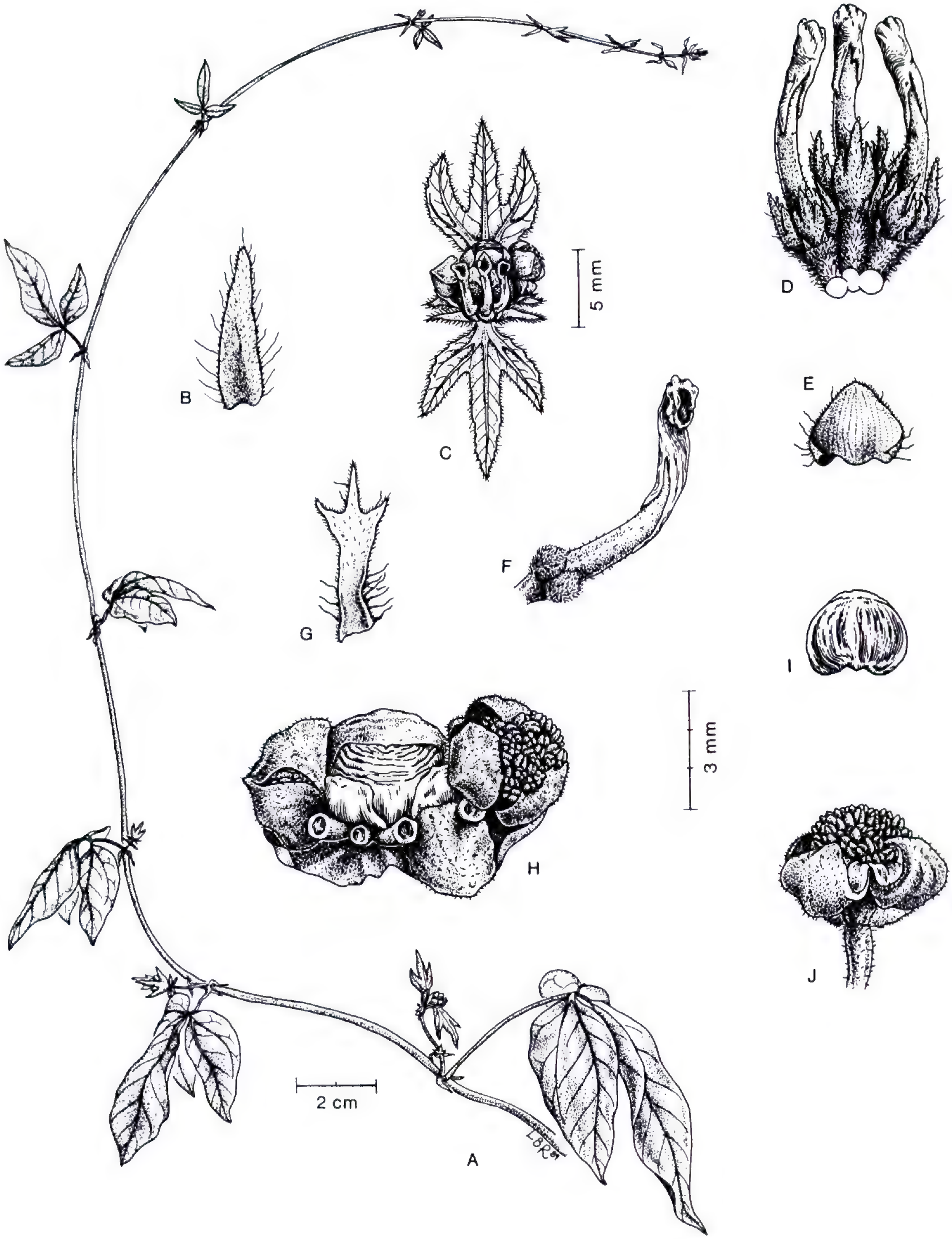

FIGURE 1. *Dalechampia allemii*.—A. Flowering branch.—B. Stipule.—C. Inflorescence at anthesis.—D. Pistillate cymule.—E. Abstaminate pistillate bract.—F. Pistillate flower (calyx removed).—G. Fruiting sepal.—H. Staminate subinflorescence.—I. Resiniferous bractlet.—J. Staminate flower.

in its small unguiculate involucral bracts, suppressed adstaminate pistillate bractlets, staminal involucel with only 3 well-developed segments, and pistillate sepals with usually a single pair of lateral lobes. The small size of the involucral bracts is reminiscent of *D. micromeria* Baillon of southern Brazil, but in that species the bracts are differently shaped, the stamens fewer (10–25), and styles shorter (2–4 mm). In the treatment by Pax & Hoffmann (1919), *D. allemii* would key down near *D. olfersiana* Muell. Arg.; however, that species is more heavily pubescent and has nonunguiculate bracts and clavate styles. Somewhat more similar in appearance to *D. allemii* is *D. clausseniana* Baillon, which also has nonglandular pistillate sepals; however, that species differs in its larger nonunguiculate involucral bracts, well-developed adstaminate pistillate bractlets, staminate involucel with 2 entire lips, and pistillate sepals with 4–7 pairs of lateral lobes.

It is a great pleasure to dedicate this distinct new species of *Dalechampia* to Antonio Allem, of EMBRAPA/CENARGEN in Brasília. Dr. Allem has made substantial contributions to the systematics of Brazilian Euphorbiaceae and is the leading authority on the taxonomy of the genus *Manihot*. The dedication is also especially appropriate because Dr. Allem was the first collector of the species in 1978 and has published the first critical reassessment of the taxa of subsect. *Triphyllae* since the treatment of Pax & Hoffmann (Allem & Waechter, 1977).

Relationships among the species of *Dalechampia* subsect. *Triphyllae* as defined by Webster & Armbruster (1990) require further study; such species as *D. clausseniana*, *D. cissifolia*, and *D. heteromorpha* are highly variable, and species limits are uncertain. The following key to the Brazilian species of subsect. *Triphyllae* should aid in locating *D. allemii* as far as gross morphological characters are concerned. Morphological terminology follows the treatment of Webster & Armbruster (1990).

Dalechampia subsect. **Triphyllae** (Pax & Hoffm.) Webster & Armbruster, Bot. J. Linn. Soc. (in press). *Dalechampia* sect. *Triphyllae* Pax & Hoffm., Das Pflanzenreich IV. 147. XII(Heft 68): 13. 1919. TYPE: *Dalechampia triphylla* Lam.

Twining vines, indumentum often sparse; leaves 3-foliolate (rarely 5-foliolate), sometimes also with simple leaves; floriferous shoots axillary; bracts greenish, unlobed or 3-lobed; staminate involucel with 7–11 flowers; stamens 10–100; pistillate sepals 6–12, entire to deeply pinnatifid; seeds smooth.

TENTATIVE KEY TO THE BRAZILIAN SPECIES OF SUBSECT. *TRIPHYLLAE*

1a. Leaves 3-foliolate; seeds 2.8–3.5 mm long.
  2a. Pistillate sepals oblong or obovate, with broad rachis (3–3.5 mm) in fruit, rachis much broader than lateral teeth (mostly 0.5–1 mm); foliage and involucral bracts nearly glabrous ..... *D. triphylla* Lam.
  2b. Pistillate sepals linear-lanceolate, with narrow rachis (not broader than 1.5 mm) in fruit, lateral teeth mostly broader than rachis.
    3a. Pistillate bractlets not glandular-capitate on margins.
      4a. Pistillate sepals without glandular-capitate lobes.
        5a. Involucral bracts unguiculate; adstaminate pistillate bractlets suppressed; pistillate sepals mostly with only 1 pair of lateral lobes; staminate involucel 3-lobed; stamens 50–80 ..... *D. allemii* Webster
        5b. Involucral bracts rounded or cordate at base; adstaminate pistillate bractlets developed; pistillate sepals mostly with 4 or more pairs of lateral lobes; staminate involucel 2-lipped, scarcely lobed.
          6a. Stylar column slender, not clavate; ovary strigose; stipules 3–4 mm long ..... *D. clausseniana* Baillon
          6b. Stylar column clavate; ovary villose; stipules 6–8 mm long ... *D. olfersiana* Muell. Arg.
      4b. Pistillate sepals with glandular-capitate lobes.
        7a. Fruiting sepals 12–15 mm long; fruiting peduncle mostly not longer than 1 cm ..... *D. cissifolia* Poeppig
        7b. Fruiting sepals shorter; peduncle generally longer.
          8.a Involucral bracts usually longer than 1 cm; stamens mostly more than 25 per flower.
            9a. Leaves monomorphic, all tripartite; involucral bracts 3-lobed; stamens 30–60.
              10a. Involucral bracts 3-lobed; fruiting sepals 3.5–5 mm long ..... *D. meridionalis* Muell. Arg.
              10b. Involucral bracts unlobed or trifid at tip; fruiting sepals 7–8 mm long ..... *D. bangii* Pax & K. Hoffm.
            9b. Leaves dimorphic, both tripartite and unlobed; bracts unlobed or 3-lobed; stamens less than 30; fruiting sepals 5–6 mm long ..... *D. burchellii* Muell. Arg.
          8b. Involucral bracts mostly ≤ 1 cm long, 3-lobed; stamens 10–25; styles 2–4 mm long, glabrous; leaves all tripartite ..... *D. micromeria* Baillon

3b. Pistillate bractlets glandular-capitate on margins; stamens 30 or more; leaves pubescent beneath, all tripartite; involucral bracts 3-lobed ..... *D. stenosepala* Muell. Arg.
1b. Leaves 5-foliolate; seeds longer than 4 mm ..... *D. regnellii* Muell. Arg.

Fieldwork in Bahia was made possible through a grant from the National Science Foundation and the collaboration of Dr. Allem and personnel of EMBRAPA/CENARGEN, Brasília. The illustrations were drawn by Leslie Randall.

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FOUR NEW SPECIES OF *ELAPHOGLOSSUM* (ELAPHOGLOSSACEAE) FROM VENEZUELA

In a series of papers (Mickel, 1985, 1987, 1990) I published 37 new taxa of *Elaphoglossum* from Venezuela. Specimens sent recently for identification included four more novelties, making a total of 107 species and three subspecific taxa known from that country.

Elaphoglossum polyblepharum Mickel, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atures, W side of valley of Río Coro-Coro, 8 km NNW of settlement of Yutaje, 05°41′N, 66°08′30″W, 1 Mar. 1987, *Liesner & Holst 21517* (holotype, NY; isotype, MO). Figure 1A.

Ab *E. erinaceo* frondium squamis brevioribus rubrobrunneis necnon laminae facie abaxiali squamosa diversum.

Rhizome compact, 4–6 mm diam.; rhizome scales linear-lanceolate, orange, ca. 5 mm long, entire; phyllopodia lacking; fronds approximate, 30–40 cm long, 3.5–4.6 cm broad; stipe ¼–⅓ the frond length, densely clothed with patent, reddish brown, subulate scales 4–6 mm long; blade narrowly elliptic, papyraceous, apex caudate, base broadly cuneate; veins evident, free, ca. 1 mm apart, at 75° angle; hydathodes lacking; blade scales reddish brown, subulate, liberally distributed on abaxial surface, 1–2 mm long, more concentrated on margin, 1.5–2 mm long, and costa, 2–3 mm long, lacking on the adaxial surface; fertile fronds unknown.

Epipetric in wet forests, 900–1,000 m.

Additional specimens examined. VENEZUELA. AMAZONAS: Dept. Atures, same locality as type, *Liesner & Holst 21405* (MO, NY); Dept. Río Negro, Cerro Aratitiyope, 02°10′N, 65°34′W, *Steyermark et al. 130312* (NY).

Elaphoglossum polyblepharum differs from *E. erinaceum* (Fée) Moore in having frond scales reddish brown rather than black-brown, these scales more dense on stipe, conspicuously present on laminar surface, and shorter on margins (1.5–2 mm long vs. 3–4 mm) and costa (2–3 mm long vs. 4–6 mm), and the rhizome scales lighter orange and shorter (ca. 5 mm long vs. 15–20 mm).

Elaphoglossum heteroglossum Mickel, sp. nov. TYPE: Venezuela. Portuguesa: Dept. Sucre, La Divisoria de la Concepción, 09°18′N, 70°06′W, 23–26 Oct. 1985, *Ortega et al. 2748* (holotype, UC; isotype, NY). Figure 1B.

Lamina utrinque glabra nisi stipite costaque squamis subulatis et margine squamulis lanceolatis provisis praestans.

Rhizome short-creeping, 3–5 mm diam.; rhizome scales linear-lanceolate, orange-tan, 1.5–2 mm long, with sparse hair-teeth; phyllopodia lacking; fronds approximate, 30–40 cm long, 2.9–3.4 cm broad; stipe ¼–⅙ the frond length, with scales subulate, patent, 2–2.5 mm long, brown; blade narrowly elliptic, papyraceous, apex acuminate, base narrowly rounded; veins evident, free, ca. 1.5 mm apart, at 60–70° angle; hydathodes lacking; blade scales on adaxial margin lanceolate, brown, 1–2 mm long, appressed, on abaxial costa subulate, brown, spreading, 2–2.5 mm long, abaxial lamina subglabrous, with simple to stellate trichomidia 0.1–0.2 mm long; fertile fronds much smaller than the sterile (½–⅓ the length), stipe ½ the fertile frond length, blade narrowly elliptic, 8–11 mm broad; fertile blade lacking scales on costa, margin, or among sporangia.

Terrestrial in cloud forests, 1,500–1,800 m.

Elaphoglossum heteroglossum resembles *E. erinaceum* in the subulate scales of stipe and costa but is distinct in the small lanceolate marginal scales vs. long subulate ones, and the much smaller fertile fronds.

Elaphoglossum xiphoides Mickel, sp. nov. TYPE: Venezuela. Bolívar: a la cuenca media del Río Paragua, 06°03′N, 63°47′W, 13 June 1987, *Stergios 10310* (holotype, NY). Figure 1C.

Ab *E. rhynchophyllo* laminae squamis ovatis gilvis et squamis intersporangialibus nullis abstans.

Rhizome creeping, 1–1.5 mm diam.; rhizome scales linear-lanceolate, orange-tan, ca. 3 mm long, entire; phyllopodia present but indistinct and covered by scales; fronds 6–10 mm apart, 5–7 cm long, 1–1.3 cm broad; stipe ⅕–⅓ the sterile frond

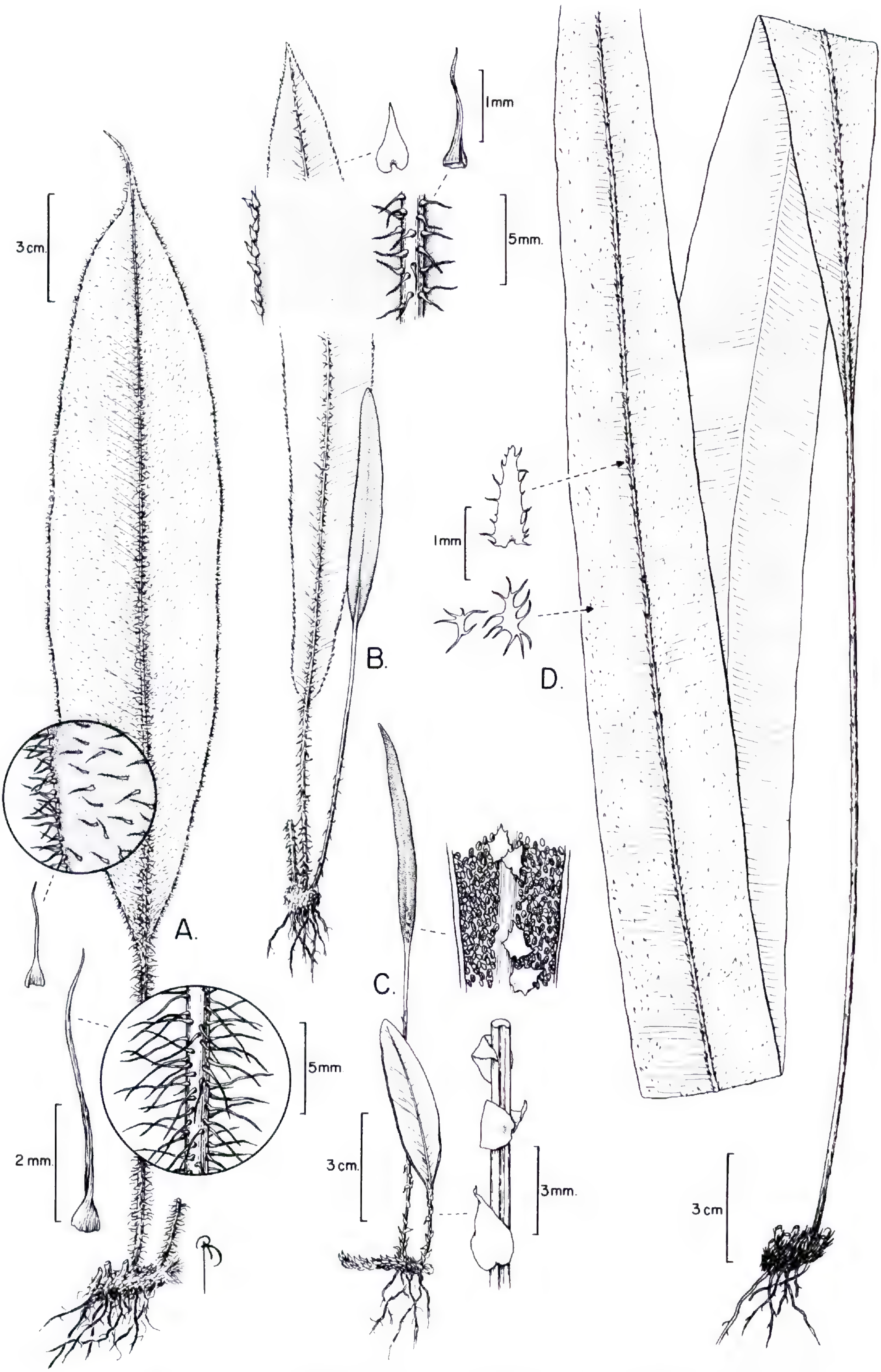

FIGURE 1. —A. *Elaphoglossum polyblepharum.* —B. *E. heteroglossum.* —C. *E. xiphoides.* —D. *E. zosteriformis.*

length, with scales ovate-lanceolate, orange-tan, spreading, ca. 3 mm long; blade elliptic to lanceolate, subcoriaceous, apex obtuse, base cuneate; veins evident, 0.8–1 mm apart, at ca. 60° angle; hydathodes lacking; blade scales scattered, orange-tan, 1–2 mm long on abaxial costa, otherwise blade glabrous; fertile frond longer than sterile (ca. twice as long), stipe ½–⅗ the fertile frond length, blade linear, 5 mm broad; intersporangial scales lacking. Terrestrial in wet forests, 175 m.

Elaphoglossum xiphoides is similar to *E. rhynchophyllum* Christ in blade shape of fertile and sterile fronds, but the blade scales in the former are tan, ovate, sparse on midvein, and intersporangial scales are lacking whereas in the latter the blade scales are black, linear, dissected, and intersporangial scales are abundant. The phyllopodium is indistinct but present in *E. xiphoides* whereas it is lacking in *E. rhynchophyllum* and other members of the *E. squamipes* complex. It also resembles *E. minutum* (Pohl) Moore in the tan scales and the presence of a phyllopodium, but the fertile blade is acuminate rather than obtuse, the rhizome is longer-creeping, and it occurs at a much lower elevation (175 m vs. over 3,000 m).

Elaphoglossum zosteriformis Mickel, sp. nov. TYPE: Venezuela. Bolívar: Río Caneracuni, entre Caneracuni y la boca, 04°30′N, 63°42′W, 13–26 Apr. 1988, *Stergios 11930* (holotype, NY; isotype, UC). Figure 1D.

Ab *E. laminarioide* laminae stipitisque squamis linearilanceolatis distans.

Rhizome compact, 5 mm diam.; rhizome scales linear-lanceolate, black-brown, lustrous, entire; phyllopodia present; fronds approximate, ca. 95 cm long, 4.8 cm broad; stipe ¼ the frond length, with scales loosely appressed, linear-lanceolate, 1–3 mm long, cilio-denticulate, tan, imbricate to somewhat deciduous; blade linear-elliptic, chartaceous, apex lacking, base narrowly cuneate; veins evident, 1 mm apart, at 80° angle; blade scales adaxially lacking except for a few 1–2 mm long, cilio-denticulate scales on costa, abaxially with scattered (touching but not overlapping) dissected scales ca. 1 mm long, linear-lanceolate, the teeth longer than the scale body width, orange-tan, costa scales linear, 1–2 mm long, cilio-denticulate with teeth shorter than the scale body width; fertile fronds unknown.

Epiphytic in wet forests of "tierra firme y riberenas," elevation unknown.

In the long, narrow blade *E. zosteriformis* resembles *E. laminarioides* (Bory) Moore, but the former has linear-lanceolate scales on the blade and stipe whereas the latter has round, peltate scales.

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A NEW SPECIES OF *ARISTOLOCHIA* (ARISTOLOCHIACEAE) FROM VENEZUELA

Very little is published on the *Aristolochia* species of Venezuela. No floristic treatment exists and none of the available revisions treat all the Venezuelan species (Ahumada, 1967; Hoehne, 1942; Pfeifer, 1966). Bazzolo & Pfeifer (1978) revised the herbaceous, efimbriate species, but all other species must be identified using Hoehne (1942). This makes the identification of Venezuelan aristolochias unusually difficult. The following species was first collected in 1962, but only now can it be confidently described as new.

Aristolochia melgueiroi Barringer & Guánchez, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Dept. Atures, along road between damsite of Río Cataniapo and Gavilán, 35–40 km SE of Puerto Ayacucho, 200 m, 11 May 1980, *Steyermark, Davidse & Guánchez 122297* (holotype, VEN; isotypes, F, MO). Figure 1.

Species *Aristolochiae killipianae* O. Schmidt affinis, sed foliis ovatis, pseudostipulis nullis, floribus rectis, utriculis ovoideis, tubis usque ad 12 mm longis differt. Item *A. triangulari* Cham. affinis, sed foliis ovatis cordatis, pseudostipulis nullis, floribus rectis, tubis ad 12 mm longis, seminibus 6–7 mm longis descrepat.

Liana; young stems slightly tomentose, glabrescent, ridged, the nodes swollen. Pseudostipules absent. Leaves alternate; petioles 10–30 mm long; laminas ovate, 7–19 × 3–8 cm, glabrous above, slightly pilose and glabrescent beneath, the base cordate, the sinus 6–17 mm deep, the apex acuminate. Flowers solitary in axils of young growth or solitary on axillary branches to 10 cm long, with a basal bract 3–7 mm long; pedicel and ovary 7–10 mm long, pilose; calyx green marked with brown-purple lines, the utricle ovoid, 5–7 × 4 mm, the tube straight, 9–12 mm long, the limb broadly funnelform, not reflexed, broadly ligulate above, spreading, 12–16 × 9–14 mm, apiculate, yellowish green marked with brown lines and brown-purple to madder-brown spots toward the mouth of the tube, with a broad orange-yellow spot near the apex; gynostemium coroniform, 6-lobed. Capsule ovoid, to 5 cm long, 3–4 cm wide; seeds flat, subcordate, broadly winged, 6–7 × 9–10 mm.

Additional specimens examined. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Dept. Río Negro, forest and roadside 5–6 km NE of San Carlos de Río Negro, 120 m, 12 Apr. 1979, *Liesner 6561* (MO, VEN); Solano, Río Casiquiare, 20 km NE of San Carlos de Río Negro, 120 m, *Liesner 7373* (MO, VEN); IVIC study site, 4 km NE of San Carlos de Río Negro, 120 m, 01°52′N, 67°02′W, 24 Jan. 1980, *Liesner 8663* (MO, VEN); Dept. Atures, Alrededor de comunidad indígena Piaroa en raudal "ceguera," margen izquierda del Río Autana, 100 m, 04°48′N, 67°28′W, 13 Nov. 1984, *Guánchez et al. 3574* (MO, TFAV, VEN). BOLÍVAR: entre la quebrada Los Brasilieros y el camino hacia Playa Blanca y el Río Uaiparú, SE of Icabarú, 450 m, 17 Dec. 1978, *Steyermark et al. 117728* (F, MO, VEN).

This species is dedicated to Emigdio Melgueiro, assistant at TFAV, in acknowledgment of his valuable contributions to the botanical exploration of the Territorio Federal Amazonas in southern Venezuela. *Aristolochia melgueiroi* has been found in the Venezuelan Guayana between 100 and 450 m, mainly in open and disturbed sites such as roadsides and secondary vegetation ("rastrojos"). *Aristolochia melgueiroi* is part of the *A. triangularis* Cham. complex (Schmidt, 1935), which also contains *A. pseudotriangularis* O. Schmidt, a Bolivian species, and *A. killipiana* O. Schmidt, from upland Peru. All the species in this complex are woody lianas with axillary flowers. The flowers are usually less than 3 cm long and have a broadly ovate limb marked with purple spots. *Aristolochia melgueiroi* can be distinguished from all other species in this complex by its lack of pseudostipules. It can be distinguished from *A. triangularis* and *A. pseudotriangularis* by its ovate leaves with deep, basal sinuses and from *A. killipiana* by its smaller utricle, straight flowers, and ovate leaves.

Aristolochia melgueiroi is vegetatively similar to *A. acutifolia* Duchartre, a native of the Amazon basin. However, *A. acutifolia* has flowers with a narrow, ligulate limb that lacks the conspicuous orange-yellow spot at the apex. *Aristolochia melgueiroi* might also be confused with the recently described *A. guianensis* Poncy from French Guiana (Poncy, 1988). The mature leaves of *A. guianensis* have longer petioles and a more triangulate lamina than *A. melgueiroi*, but the juvenile leaves are similar. The flowers of the two species are very

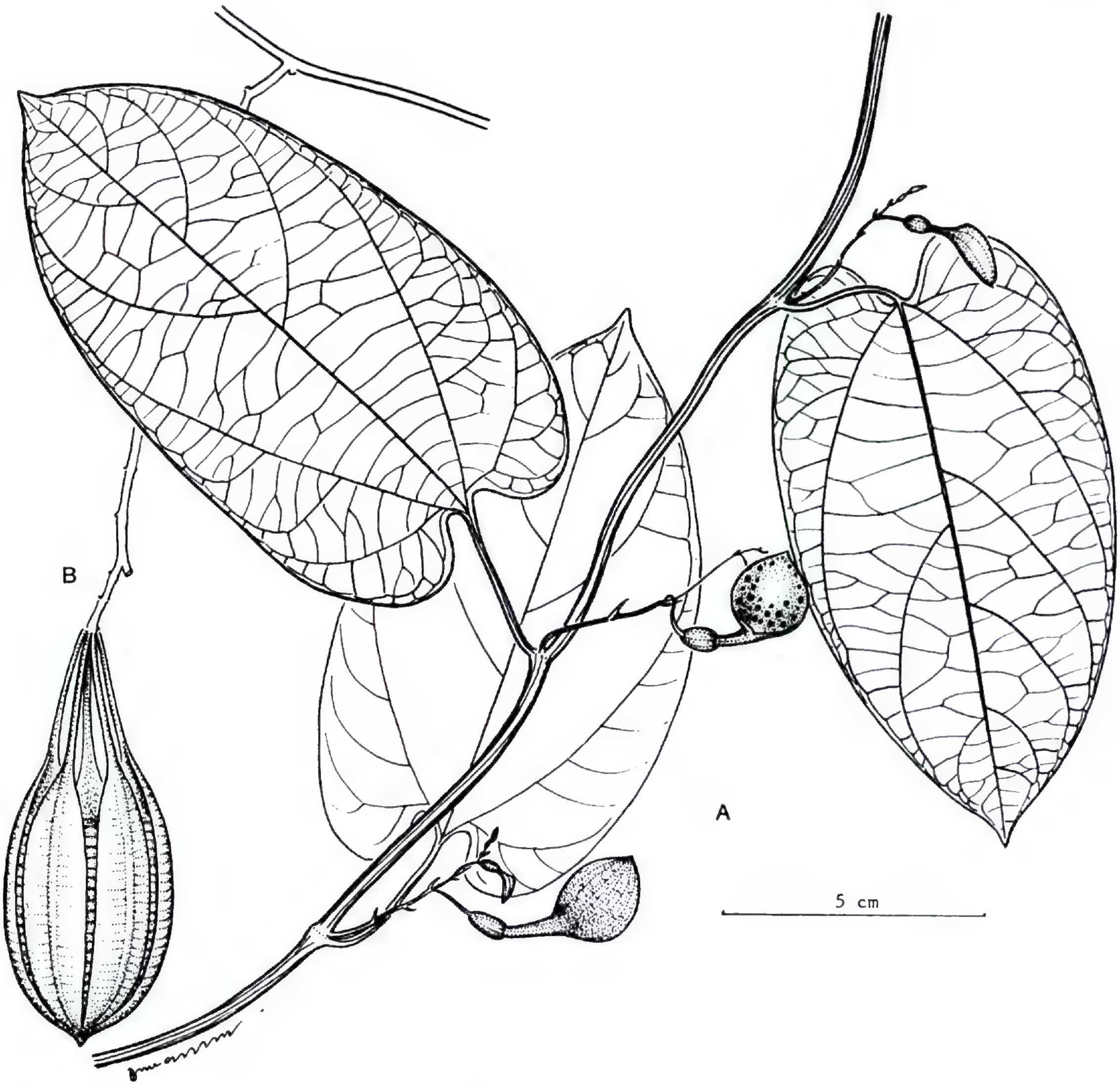

FIGURE 1. *Aristolochia melgueiroi.*—A. Flowering branch.—B. Fruit.

different, though. The flowers of *A. guianensis* have a large, unilabiate limb borne perpendicular to the tube and 5–8 cm long peduncles.

We thank Paul Berry and Bruce Holst (MO), who helped coordinate our efforts, and the curators of F, MO, NY, TFAV, and VEN, who allowed us to study their collections.

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ON THE TYPIFICATION OF *BIGNONIA CRUCIGERA* L. (BIGNONIACEAE)

In the first edition of *Species Plantarum*, Linnaeus (1753: 624) proposed *Bignonia crucigera*, taking as his polynomial *Bignonia foliis conjugatis cirrhosis*; *foliolis cordatis*; *foliis imis ternatis*, a reorganized form of the phrase name he had first proposed in *Viridarium Cliffortianum* (1737a: 60) and which was used again in his *Hortus Cliffortianus* (1738: 317) and van Royen's *Florae Leydensis* (1740: 289). He also cited two synonyms, one from Gronovius (1739: 73), the other from Morison (1699: 612, erroneously cited as 672). Lastly, Linnaeus added a brief description: "Caulis volubilis, scaber, transversim dissectus crucem repraesentat," and the statement "Habitat in Virginia and australiori America."

There are no specimens in any of the Linnaean herbaria, nor in the Clifford herbarium (BM), associated with this name. There are, however, three elements associated with it. Two are linked to the synonymy, a specimen cited by Gronovius, *Clayton 100* (BM), and a Morison (1699) figure, *s. 15. t. 3. f. 16.*

The third element is a plate from Charles Plumier, not published until three years after *Species Plantarum* (Plumier, 1756), and hence not cited directly in the protologue. Plumier had made more than 1,200 drawings on trips to the West Indies in 1689–1690 and 1696–1697 (see Stafleu & Cowan, 1983). The Dutch naturalist Hermann Boerhaave had acquired copies of more than 500 of them, and it was these copies that Linnaeus examined while in Leiden in 1738 (Polhill & Stearn, 1976). Linnaeus recorded his observations in a copy of the first edition of *Genera Plantarum* (Linnaeus, 1737b), now in the library of the Linnean Society of London. While it was known that Linnaeus had examined Plumier plates prior to 1753, Polhill & Stearn (1976) were the first to establish the connection between the Plumier copies in Holland, the annotated *Genera Plantarum*, and the descriptions in *Species Plantarum*.

Linnaeus wrote the notes on the *Bignonia* plate opposite p. 179:

> Bignonia scandens bifolia & trifolia, ligno crucea figurato. Plum. mss. Obs: caulis volubilis scaber, dissectis cruceum depictam exhibet.

He took the observation, with minor rephrasing, for his descriptive sentence in 1753. Although the plate was not cited until the second edition of *Species Plantarum* (Linnaeus, 1763), where it was cited from the published source (Plumier, 1756), the commentary provides the necessary link confirming that the plate (now at Groningen) is original material, and that it influenced Linnaeus's concept of the species as published in 1753.

The name *Bignonia crucigera* has been associated with three taxa in as many genera, each of which is represented in the original material. The information, summarized here, is discussed in greater detail by Gentry (1975). The Gronovian specimen, *Clayton 100* (BM), is a collection of what is now known as *Bignonia capreolata* L., a connection recognized by Small (1903), who treated *B. capreolata* as a synonym of *B. crucigera*. The Morison illustration is of a fruit and single seed of *Bignonia echinata* Jacq. (= *Pithecoctenium crucigerum* (L.) A. Gentry). The Plumier plate illustrates *Tanaecium crucigerum* Seem. In his circumscription, Seemann (1856), citing Linnaeus (1763), excluded all of Linnaeus's synonymy for *B. crucigera* except Plumier (1756).

Gentry (1975) attempted to resolve the problem by typifying the name and thereby fixing its usage. Several of the options were unappealing. Selecting *Clayton 100* would have resulted in the displacement of the North American *Bignonia capreolata* and, writing prior to Polhill & Stearn (1976), it was understandable that Gentry should not have regarded the Plumier plate as original material. It therefore seemed impossible to typify the name in the sense of *Tanaecium crucigerum*, even if such a choice were deemed desirable.

Gentry argued that the most reasonable option was to return to Linnaeus's original concept of the species, reflected in the protologue in *Hortus Cliffortianus*. Linnaeus cited two synonyms there, that of Morison (1699), cited again in 1753, and a name from Miller's (1737) *Gardeners Dictionary*, *Bignonia scandens tetraphylla, fructu maximo echinato*. This appears to relate to the same sort of plant illustrated by Morison, and there is a Miller specimen at BM, possibly contemporary, belonging to this species. Gentry argued that the Miller specimen was an eligible syntype because it was tied to a citation in Linnaeus's original, that is, 1738,

description. The designation of the specimen rather than the illustration was based on Recommendation 7B-5, in the "Guide to the Determination of Types" then in effect (Stafleu et al., 1972), which stated that specimens were to be selected over illustrations.

Unfortunately, whatever its connection to *Hortus Cliffortianus*, the Miller specimen cannot, under the present Code (Greuter et al., 1988), be considered original material, as Linnaeus never saw it, and it is hence ineligible for selection as the lectotype. Moreover, the expanded synonymy in *Species Plantarum* indicates that Linnaeus's concept of *Bignonia crucigera* changed between 1738 and 1753, and there is no direct evidence that he still considered the Miller name a synonym by 1753.

Although the lectotypification on the Miller specimen cannot stand, one of the eligible elements, the Morison plate, illustrates the same sort of plant. Therefore, *Bignonia crucigera* L. is here lectotypified on *PseudoApocynum folliculis maximis obtusis. . . , s. 15. t. 3. f. 16* (Morison, 1699). This typification preserves current usage of *Pithecoctenium crucigerum* (L.) A. Gentry.

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STUDIES IN MIDDLE AMERICAN BROMELIACEAE I

Smith & Downs (1974) in their monograph of Bromeliaceae subfamily Pitcairnioideae included 56 species of *Pitcairnia* from Mexico and Central America. Since that time four previously unreported species were collected from the area, including one originally thought to be native to Brazil (Zamudio, 1988), and five new species have been described (Luther, 1987a, b; Rauh, 1986; Smith & Read, 1975). In addition, we herein propose two new taxa, *P. beachiae* and *P. virginalis*, bringing the number of *Pitcairnia* species for Mexico and Central America to 67. It is likely that this number will continue to fluctuate as our knowledge of the flora expands, due not only to new species, but also to reinterpretations of species limits (cf. McVaugh, 1989).

Pitcairnia beachiae Utley & Burt-Utley, sp. nov. TYPE: Costa Rica. Puntarenas: Valle de General, 300 m, collected 12 May 1974, flowered in cultivation April 1984, *Beach 74-25* (holotype, US; isotypes, CR, F, MO). Figure 1.

Folia petiolata persistentia spinescentia. Scapus decurvus abrupte bracteae persistentes internodia superantes. Inflorescentia 4.5–10 cm longa densiflori. Petala lutea. Ovarium circa ¾ inferum.

Epilithic or terrestrial herbs, to about 1.5 m tall in flower. Leaves dimorphic, persistent; outer leaves sheathing, bladeless; inner leaves 1–1.7 m long, subpetiolate to petiolate; sheaths 1–1.5 cm long, 4–4.5 cm wide, serrulate, light brown to stramineous with brown shaggy pubescence, contracting abrubtly into the petiole; petiole 20–60 cm long, 0.4–1.2 cm wide, scattered spinose-serrate, becoming strongly involute on drying; blade with a pronounced midrib, plicate, narrowly elliptic to lance-elliptic, 69–100 cm long, 3–6 cm wide, apically attenuate, glabrous adaxially, densely pale pubescent abaxially, marginally scattered spinulose-serrulate becoming subdensely serrulate apically, chartaceous. Scape 22–32 cm long, 5–7 mm diam. (1–1.5 cm diam. in living material), erect for 5–7 cm and then abruptly decurved, brown floccose pubescent; bracts 3.5–36 cm long, exceeding the internodes but divergent to subspreading and the scape exposed, pale pubescent to locally glabrous, lower bracts subfoliaceous and scattered spinose-serrate, middle and upper bracts much reduced and entire. Inflorescence simple, 4.5–10 cm long, 5–6 cm diam., horizontal or slightly ascending, densely spicate to subglobose, polystichously many-flowered. Floral bracts exceeding the sepals, erect, ovate to elliptic, 2.3–3.5 cm long, (0.7–)1.2–1.5 cm wide, acuminate, entire, pink drying brown, finely evanescently pubescent. Flowers erect to divergent, sessile; sepals coriaceous, triangular, 2.6–2.9 cm long, 1–1.2(–1.5) cm wide, short attenuate, brown floccose abaxially, glabrous adaxially, much thickened basally, thickened to distinctly asymmetrically keeled medially; corolla narrowly tubular, curved (abaxially?) in distal ⅓ at anthesis; petals basally appendaged, dissimilar, straight to falcate, narrowly obovate, ovate or elliptic, 6–6.4 cm long, 0.7–1.4 cm wide, yellow, basally attenuate, apically acute and mucronulate; stamens included, filaments 3–4.6 cm long, flattened, anthers basifixed, narrowly hastate, 1.3–1.6 cm long; ovary about ¾ inferior, 0.9–1.3 cm long, 0.75–1 cm diam.; style 4.5–5.5 cm long.

This species is named in honor of Eloise Beach of Orlando, Florida. In addition to collecting this species for the first time, Eloise's unstinting studies of the Bromeliaceae have added considerably to our horticultural and botanical knowledge of the family. *P. beachiae* is most similar to *P. quesnelioides* L. B. Smith from Colombia and the Peruvian *P. fimbriato-bracteata* Rauh in its densely flowered, simple inflorescences, persistent petiolate armed leaves, and sessile to subsessile flowers with appendaged petals and largely inferior ovaries. It is easily distinguished from these taxa by its persistent floral bracts, in contrast to the deciduous or early decomposing floral bracts of the latter two species. It further differs from *P. quesnelioides* in having persistent upper scape bracts and a shorter inflorescence (4.5–10 cm vs 15 cm). In addition, *P. beachiae* differs from *P. fimbriato-bracteata* in its scape bracts, which much exceed the internodes and yellow flowers; in contrast the latter species has red flowers and scape bracts that are conspicuously shorter than the internodes. Despite our numerous attempts we have been unable to

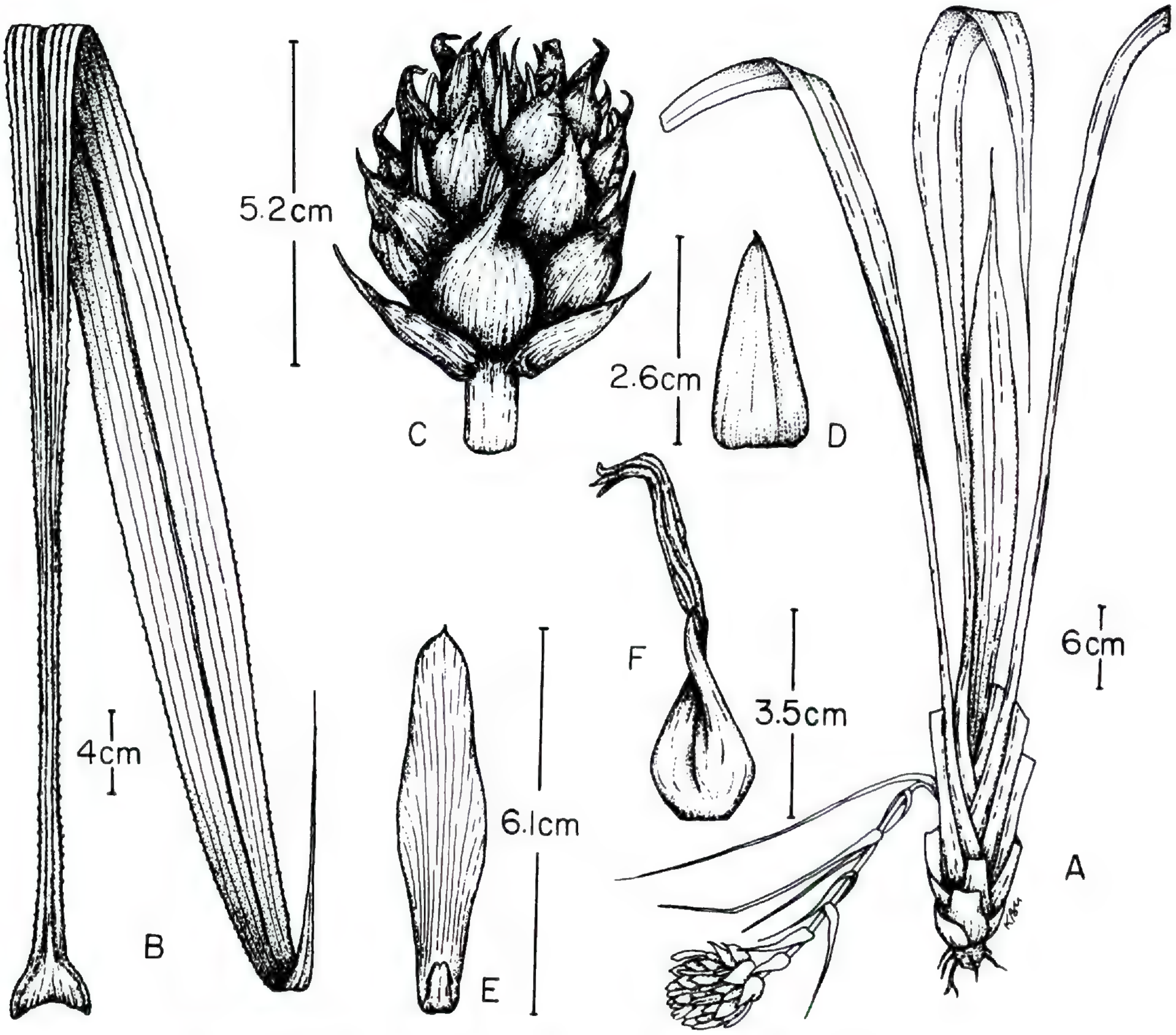

FIGURE 1. *Pitcairnia beachiae* Utley & Burt-Utley.—A. Habit.—B. Leaf.—C. Inflorescences.—D. Sepal.—E. Petal.—F. Flower post-anthesis. From *Beach 74–25*.

collect fertile material at the type location, even though vegetative individuals are regularly encountered.

Pitcairnia virginalis Utley & Burt-Utley, sp. nov. TYPE: Mexico. Oaxaca: steep roadbanks along MEX 175, 29.7–30.1 mi. N of N side of Pochutla or 5.1–5.5 mi. N of turnoff to Pluma Hidalgo, 4,900–5,000 ft., 17 July 1989, *Utley & Utley 8400* (holotype, MEXU; isotypes, MICH, MO, US). Figure 2.

Folia heteromorpha. Laminae magiores deciduae. Scapus 32–65 cm longus bracteae infernae foliaceae. Inflorescentia 7–10 cm longa ante florenti circa 30 cm ubi fructificans. Bracteae florales 4.5–6.5 cm longae late ovatae vel anguste ellipiticae acutae chloroleucae pubescentes pallentes. Petala alba appendiculata. Ovarium circa ½ inferum.

Herbs, terrestrial or epilithic on humus-covered rocks; 60--100 cm tall in flower. Leaves trimorphic: the outer two types with broadly triangular, tightly overlapping sheaths, these entire proximally becoming serrate near junction with blade, castaneous, densely white to pale ferrugineous lanate abaxially, glabrous to glabrescent adaxially; some with blades persistent, spiniform, pectinate-serrate, 3–5 cm long, others with apparently linear(?), deciduous blades which disarticulate 2–4 cm above the sheath, persistent portion of blade 1–2.5 cm wide, densely serrate (characters of deciduous portion unknown): inner leaves and lower scape bracts entire or weakly serrate basally: sheaths ovate, 4–5.5 cm long, 2.2–3 cm wide, pale, scattered pubescent abaxially; blades narrowed above the sheath, often with a tendency to disarticulate at the sheath upon drying, elongate-triangular or elliptic to narrowly ovate, 30–36 cm long, 2.5–3 cm wide, scattered pale floccose abaxially. Scape curved-erect,

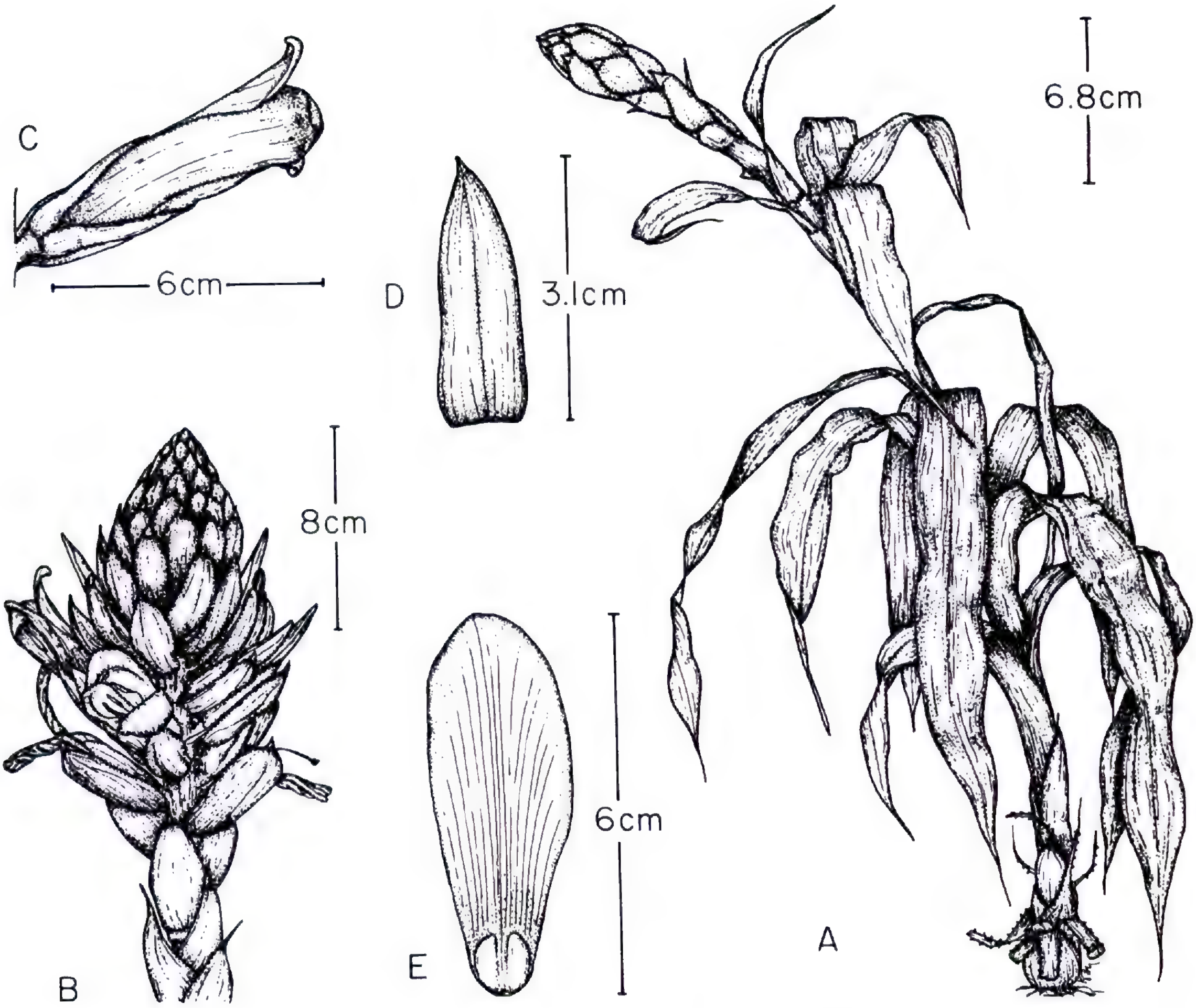

FIGURE 2. *Pitcairnia virginalis* Utley & Burt-Utley.—A. Habit.—B. Inflorescence.—C. Flower at anthesis.—D. Sepal.—E. Petal. From *Utley & Utley 8400.*

32–65 cm long, scattered to subdensely pale floccose; lower bracts foliaceous, the upper reduced and subfoliaceous, 21–31 cm long, glabrous adaxially, scattered pale floccose abaxially, sheaths inflated, clasping, blades divergent to drooping-recurved above middle. Inflorescence simple, racemose, 7–10 cm long pre-anthesis, elongating to about 30 cm post-anthesis. Floral bracts broadly ovate to narrowly elliptic, 4–6.5 cm long, 1.3–3 cm wide, becoming reduced distally, acute, pale green-white drying brown post-anthesis, adaxially glabrous, abaxially white floccose proximally, densely pale ferrugineous distally. Flowers ascending to divergent or subspreading at anthesis, pedicels 3–5 mm; sepals broadly triangular to subligulate, 2.9–3.3 cm long, about 1 cm wide, acute, subdensely brown pubescent; corolla broadly tubular to elongate-campanulate; petals basally appendaged, obovate, 5.9–6.3 cm long, 2–2.3 cm wide, white, broadly acute; stamens included, filaments 4.1–4.3 cm long, anthers basifixed, hastate, 1.4–1.5 cm long; ovary trigonous in cross section, about 1.2 cm long, 0.6–0.7 cm diam., about one-half or less inferior; style about 5–5.2 cm.

Pitcairnia virginalis is most similar to *P. abundans* L. B. Smith from Nayarit, Mexico in its heteromorphic leaves, with the larger leaf blades deciduous, elongate scape with foliaceous to subfoliaceous lower bracts and white appendaged petals. It differs in having broadly ovate to narrowly elliptic, apically acute floral bracts, 4–6.5 cm long, in contrast to the floral bracts of *P. abundans*, which are triangular to triangular-lanceolate, apically caudate-attenuate and 1.5–3.5 cm long. Moreover, sepals of *P virginalis* are generally longer (2.9–3.3 vs 2.6–3 cm) and apically acute rather than long subulate like those of *P. abundans*. *Pitcairnia virginalis* is unusual among Mexican and Central American *Pitcairnia* species in

having white, elongate-campanulate corollas, and large, pale green to white, pubescent floral bracts. In addition, the inflorescence elongates considerably post-anthesis; this change in morphology is so striking that plants at anthesis and in fruit could, on casual inspection, be taken for distinct species.

Additional collections. MEXICO. OAXACA: El Porvenir, carr. Pochutla–Oaxaca, 15 junio 1985, *R. Torres C. 6835* (MEXU); MEX 175 1.5 mi. S of La Soledad, 5,100 ft., 1 Aug. 1990, *Utley & Utley 8588* (CAS).

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STUDIES IN MIDDLE AMERICAN BROMELIACEAE II

Mezobromelia is distinguished from other members of the subfamily *Tillandsioideae* by epipetalous stamens and biappendaged petals that are agglutinate or connate for a significant portion of their length. Smith (Smith & Downs, 1977) recognized two species in the genus, and Rauh (1976, 1977) described two more. Recent collections from Costa Rica of flowering material congruent with *Vriesea splitgerberi* (*Utley & Utley 7141*) show that the petals of this species are biappendaged and connate. These characteristics, in conjunction with the polystichously flowered inflorescence branches (a condition rarely encountered in *Vriesea* but common in *Mezobromelia*), strongly suggest that this species is better treated as a member of *Mezobromelia*. Gouda (1987) presented evidence that *V. splitgerberi* is conspecific with *Tillandsia pleiosticha* and proposed the combination *Vriesea pleiosticha*. Because we consider the species to be better placed in *Mezobromelia*, we propose the following new combination.

Mezobromelia pleiosticha (Griseb.) Utley & Luther, comb. nov. *Tillandsia pleiosticha* Griseb., Nachr. Konigl. Ges. Wiss. Georg Göttingen-Augusts-Univ. 1864: 19. 1865. *Vriesea pleiosticha* (Griseb.) Gouda, Fl. Guianas, Ser. A 189: 82. 1987. TYPE: Venezuela: *Fendler 1514* (holotype, GOET).

Guzmania splitgerberi Mez, Monogr. Phan. 9: 930. 1896. *Thecophyllum splitgerberi* (Mez) Pittendr., Evolution 2: 60. 1948. *Vriesea splitgerberi* (Mez) Lyman B. Smith & Pittendr., J. Wash. Acad. Sci. 43: 403. 1954. TYPE: Surinam: *Splitgerber 966* (holotype, L).

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ANN. MISSOURI BOT. GARD. 78: 270. 1991.

ERRATUM

Erratum for *Xyris* (Xyridaceae) from the Planalto of Brazil

There has been oversight in regard to disposition and location of holotype material of *Xyris* species treated in R. Kral & M. G. L. Wanderley's (1988), "Ten novelties in *Xyris* (Xyridaceae) from the Planalto of Brazil" (Ann. Missouri Bot. Gard. 75: 352–372). The holotypes of five [*X. sceptrifera* Kral & Wanderley (*Irwin et al. 13410*); *X. seubertii* Nills. var. *espinhacae* Kral & Wanderley (*Irwin et al. 23667*); *X. obcordata* Kral & Wanderley (*Irwin et al. 27763*); *X. itambensis* Kral & Wanderley (*W. R. Anderson et al. 35879*); *X. villosicarinata* Kral & Wanderley (*Irwin et al. 19570*)], incorrectly assumed to be deposited already at UB, had not yet been sent there. The holotype of *X. pranceana* Kral & Wanderley (*Prance & Silva 58195*) is in place at MG, not at UB as was stated in the publication. Thanks to a thoughtful check by Jacquelyn Kallunki at NY, these errors were caught, the holotypes are being sent to UB, and the correct location for the holotype of *X. pranceana* is now given. The oversight is entirely mine!

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Ann. Missouri Bot. Gard. 78: 271. 1991.

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In 1991, the Missouri Botanical Garden will begin publishing a journal devoted to the establishment of new nomenclatural entities and new taxonomic synonymy. The name of the journal, *Novon*, is a made-up word meaning any nomenclatural entity at its first publication. *Novon* will include descriptions and names of new taxa, new combinations of existing names, and new names. Although the format of articles will be concise and stereotyped, ample space will be provided to discuss the taxonomic and/or nomenclatural justification for proposed nova. Taxonomic coverage will be restricted to vascular plants and bryophytes. The journal will be automatically distributed quarterly to all who receive the *Annals of the Missouri Botanical Garden*. Initally, *Novon* will not be available as a separate subscription or exchange. Beginning in 1991, the editorial policy of the *Annals of the Missouri Botanical Garden* will be changed to exclude articles devoted to nova.

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BIOLOGICAL EXTINCTION IN WESTERN ECUADOR

C. H. Dodson[1] *and A. H. Gentry*[2]

ABSTRACT

This paper documents the extent of deforestation in western Ecuador and what is known about its effect on biodiversity. Maps are provided comparing the extent of relatively undisturbed forested areas in aboriginal times, 1958, and 1988. Patterns of floristic diversity and endemism are discussed in light of the massive deforestation, and evidence of extinction of plant species from four florula sites is provided. The naturally fragmented nature of much of the western Ecuadorian forest is discussed, both in terms of evolutionary effects and implications for long-term conservation.

The forests of western Ecuador have been cited as one of the most severely threatened areas on earth in terms of biological extinction as a result of deforestation and other activities of humans (Meyers, 1986, 1987, 1988; Gentry, 1989; Simberloff, 1986). Although few precise data are readily available, clearly deforestation has left only small forest remnants. Extrapolations based on the theory of island biogeography (MacArthur & Wilson, 1967; Simberloff & Able, 1976) suggest that biological extinction in this region may have been massive.

This report is intended to provide concrete data concerning the status of forests, reserves, and extinction in western Ecuador and to suggest possible means to salvage what remains.

GEOGRAPHY, SOILS, AND CLIMATES OF WESTERN ECUADOR

The boundaries of western Ecuador have been established by geographers (Anonymous, 1980) as the Pacific Ocean to the west, the Colombian border to the north, the Peruvian border to the south, and the 900-m contour line on the Andean mountains to the east. With this definition, western Ecuador has a land area of approximately 80,000 km^2, almost a third of the total 273,000 km^2 of the present-day Republic of Ecuador. As thus defined, western Ecuador is about the size of North Carolina, while the Republic of Ecuador is similar in size to California. The majority of western Ecuador consists of a series of peneplains extending westward

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from the base of the abruptly rising Western Cordillera of the Andes. There is also a low range of coastal hills seldom exceeding 800 m in elevation.

The cold Humboldt Current moves northward along the coast and collides with the warm Panama Current moving southward. Both then move westward toward the Galápagos Islands. The earth's seasonal oscillation provides annual northward and southward shifts in the currents, which affect the climate of western Ecuador. In general, the region nearest the coast is more affected by the Humboldt Current and is drier, while the Andean foothills are moister. The southern half of the coastal region, with less than 1,000 mm annual rainfall, has a rainless period exceeding eight months (early May through early January), although a persistent cloud cover during the dry season ameliorates the temperature and dryness. Near the ocean, night fogs provide substantial atmospheric humidity, especially on the crests of the low coastal mountains. Beginning about one degree south of the equator, the coastal region becomes increasingly humid northward, varying from an annual rainfall of 2,000 mm, with a monthly minimum of 10 mm rainfall, to annual rainfall of 7,000 mm, with at least 100 mm of rain each month near the Colombian border.

The soils of the western peneplains are alluvial and volcanic in origin. Agricultural use of the lands by humans since aboriginal times has sustained large populations, and much of the region is now under intensive agriculture. The soils of western Ecuador are much richer than those of most other tropical lowland areas. Associated high productivity and turnover rates of the native forest may be in part responsible for the dynamic speciation that seems to have occurred. The rich soils make the western Ecuadorian conservational situation very different from that in most tropical regions. Instead of the common alternative of forest conservation, i.e., a few years of crops followed by abandonment, in western Ecuador the alternative to forest conservation is often productive and sustainable agriculture. This situation is somewhat analogous to that of mid-America during the middle of the last century where cultivation of rich soils nearly eliminated native prairie flora.

Vegetation Coverage

According to one of the more recent ecological maps of Ecuador (Cañadas & Estrada, 1978), based on the Holdridge (1967) system, 12 life zones occur in western Ecuador (Fig. 1). We suspect that one more life zone, a subdivision of pluvial forest, which Cañadas & Estrada did not include, may occur in the extremely wet region of northern Esmeraldas Province. Our experience, after years of collecting plant specimens and traveling throughout western Ecuador, suggests that all of the ecological maps of Ecuador are quite generalized, and we feel that many of the life zones are much more fragmented than is indicated even on the Cañadas & Estrada map. This natural fragmentation may have helped spawn the many endemics found in small habitat patches.

The prolonged dry season in the south and west generally results in a progression of desert, desert scrub, tropical thorn scrub, and a dry to very dry tropical forest as one moves inland away from the cold waters along the coast. The coastal hills are clothed with thorn scrub at the base, premontane dry forest on the slopes, and moist or wet forest on the higher crests. The original forest cover of the southern portion of the central plains was tropical dry forest. This gives way to tropical moist forest, without a clearly discernable transition zone, near 2° south latitude (near Babahoyo), and tropical moist gradually gives way to tropical wet forest north of 1° south latitude (north of Quevedo). Near Santo Domingo the moist forest is replaced by premontane pluvial forest. An extensive system of savannas, swamps, and gallery forests once existed along the large rivers that drain the Guayas basin south of 1° south latitude. Only the Santa Elena Peninsula, at the western extreme of Ecuador immediately adjacent to the cold Humboldt Current, had true desert conditions similar to those of coastal Peru and was completely lacking forest cover.

A narrow strip of perhumid cloud forest on the lowermost Andean slopes is included in western Ecuador. This forest is an extension of the Colombian Chocó pluvial forests, which are generally characterized by extremely high annual rainfall. These wet forests extend southward in increasingly narrow elevational bands along the flanks of the Andes. True lowland pluvial forest, with perhaps 8,000 mm of rain, reaches south only to near Lita, a few kilometers south of the Colombian border, at about 1° north latitude. Premontane wet forest reaches nearly to the Peruvian border, where it is reduced to a strip only a few hundred meters wide near the 900-m contour. (Other montane vegetation types exist above that contour but are not within the scope of this discussion.) In general, the moist vegetation types form broad extensions near the Colombian border but are reduced to narrow bands between 300 and 900 m elevation near the Peruvian border.

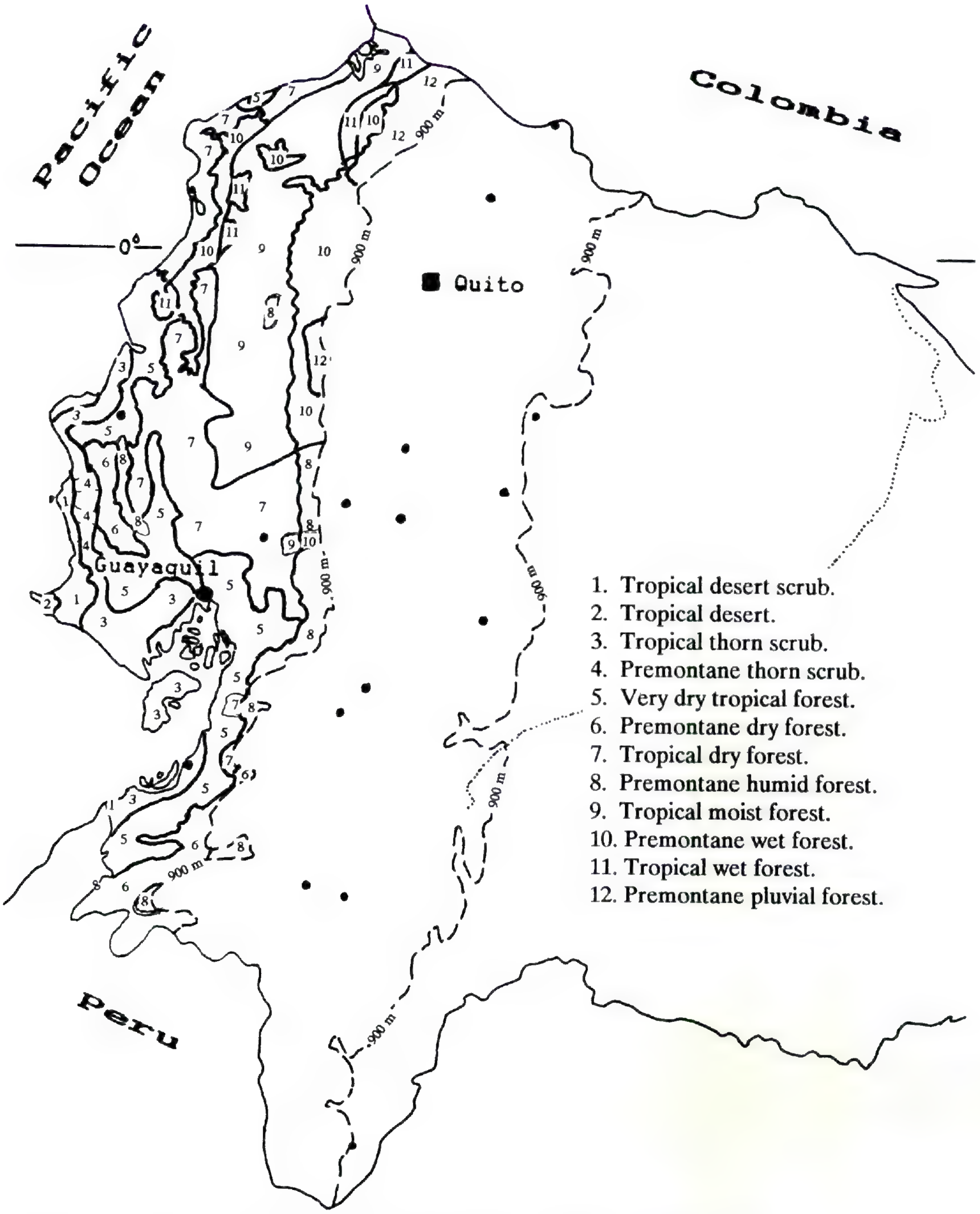


FIGURE 1. Map of life zones of western Ecuador based on Cañadas & Estrada (1978).

FLORA AND FAUNA OF WESTERN ECUADOR

Ecuador as a whole is very rich biotically. The current estimate of 20,000 vascular plant species in Ecuador (Harling, 1986) far exceeds the estimated 17,000 species (Morin, pers. comm.) known for all of North America.

Of the 12 life zones reported in western Ecuador, 10 have been studied with varying degrees of intensity. Five have been extensively sampled by

using the florula approach (see Dodson & Gentry, 1978). These include the *Flora of Rio Palenque* (1978) in tropical wet forest, the *Flora of Jauneche* (Dodson et al., 1985) in tropical moist forest, the *Flora of Capeira* (in press) in tropical dry forest, the *Flora of Centinela* (in prep.) in premontane pluvial forest, and the *Flora of Tenefuerte* (in prep.) in premontane wet forest. The Santa Elena Peninsula, with three very dry life zones (tropical desert, tropical desert scrub, and tropical thorn scrub) was studied by Svenson (1946) and Valverde et al. (1979). Valverde is presently preparing a flora of the Cerros de Colonche. This region of the dry coastal mountains has tropical thorn scrub, premontane thorn scrub, tropical dry forest, very dry tropical forest, premontane dry forest, and tropical moist forest.

Accurate estimates of the number of species of vascular plants in western Ecuador are not possible at this time, especially since two of the life zones richest in species diversity have not been sampled extensively, i.e., premontane humid and pluvial forest. Yet extrapolations of species numbers can be based on data from the areas sampled for florula preparation and from the relatively thoroughly sampled western Ecuadorian orchid flora. The five sites studied by Dodson and Gentry have a combined total of about 2,500 species. The number of orchid species found in the five florula sites is 253, closely following the 10% suggested for tropical floras worldwide (Kress, 1986). We have 2,607 orchid species cataloged for all of Ecuador, thereby also close to 10% of the estimate of 20,000 vascular plant species recently projected by Harling (1986). The 632 orchid species cataloged for lowland western Ecuador, multiplied by ten, give a rough estimate of 6,300 vascular plant species in the region.

Overall figures for fauna are not available, but data on birds show more than 1,600 species known for the country (Ridgley & Greenfield, pers. comm.), 650 of these in western Ecuador. The highest bird endemism in the world is probably in the Ecuador/Colombia western slope border area (Terborg & Winter, 1982).

ENDEMISM IN WESTERN ECUADOR

Endemism can occur at many different levels, from a single ridge top to a continent. Gentry (1986a) used the term "locally endemic" for species that have total distributions of up to 75,000 km^2. Most species endemic to western Ecuador are much more localized, occurring in only one or two ecologically appropriate forest types, with original distributional areas of less than 20,000 km^2.

By comparing distributional patterns of the species included in the florulas mentioned above, Gentry (1982a) estimated that about 20% of the flora is endemic. For example, of the 870 naturally occurring flora of Rio Palenque species with known distributions, 20% (172) are endemic to western Ecuador and another 6% to western Ecuador plus adjacent Colombia. Similar analyses of the distributional patterns of the plant species of the dry forest in the flora of Capeira show that 19% are endemic to the dry area of western Ecuador (here taken to include the phytogeographically similar adjacent northwesternmost corner of Peru). Thus, endemism of the dry forest species is essentially as high as for the wet forest ones. Dry forest plants differ in having only five species (1% vs. 6% of the Rio Palenque flora) more widely endemic to coastal Ecuador plus adjacent Colombia. In western Ecuador moist-forest species tend to be less prone to endemism than those of either dry or wet forest. Nevertheless, analysis of the 553 species of the moist-forest Jauneche florula (Dodson et al., 1985), for which we have complete identifications and distributional data, indicates that a significant 15% are endemic to western Ecuador, with an additional 2% endemic to western Ecuador plus southwest Colombia. Identifications are as yet too incomplete for our cloud forest florula sites to attempt similar analyses, but they may have even higher rates of endemism.

We conclude from the above data that if lowland western Ecuador has 6,300 naturally occurring species, around 20% of them, or 1,260 species, are probably endemic to the region. Interestingly, even though moist and dry forest florulas have a higher percentage of widespread species (respectively 47% and 50%) than does wet forest Rio Palenque (31%), the endemism rate remains similar, due to reductions in such intermediate distributional categories as Central America-to-western Ecuador (8% at Capeira and 12% at Jauneche vs. 18% at Rio Palenque).

A taxonomic breakdown of endemism figures is also of interest. At Rio Palenque 28% of the monocots are endemic vs. 19% of the dicots, but at both Capeira and Jauneche endemism of monocots and dicots is similar. At all three sites, fern endemism is much less (6–9%), and orchid endemism unusually high (24% at Jauneche, 50% at Capeira, and 28% at Rio Palenque). Much of the excess of endemic monocots at Rio Palenque is due to high representation of speciation-prone orchids. In view of their unusually rapid speciation (Gentry & Dod-

son, 1987b; Burns-Balogh & Bernhardt, 1988), an estimate of endemism based on orchids might be expected to be on the high side, even though orchids are also famous for long-distance dispersal of their minute seeds. Orchids have been relatively intensively surveyed in western Ecuador and 68 (or 27%) of the 250 orchid species known from the sites are regional endemics. Again, this would seem to agree with our estimate of around 20% endemism for the flora as a whole.

The preceding discussion addressed endemism at a regional level. However, within western Ecuador there are loci of much narrower endemism, especially on isolated ridge tops. Some of these patches of high local endemism may consist of habitat islands no more than 0.5–10 km^2. That such extreme local endemism is typical of certain tropical forests has only recently been realized (Gentry, 1982c, 1986a). The best documented case is the Centinela ridge top (see below and Gentry, 1986a). This is the first Andean foothill ridge, about 8 km east of Rio Palenque and isolated from the main Andean range farther east by a broad, flat valley about 15 km wide. The ridge is only about 20 km long and 1 km wide, an area of some 20 km^2. At its northern end it merges with the flat but higher altitude terrain formed by the less eroded outwash from the Andes of the Santo Domingo area. It is only 800 m high at its highest point and thus only 500 m higher than the valley that separates it from the Andean foothills proper. Nevertheless, it is high enough to engender a local cloud forest effect, and has a flora dramatically different from adjacent regions. Thirty-eight new species of vascular plants have already been described from this ridge top, and many additional collections appear to represent new species. Including morphotypes that we have been unable to match with named material in the herbarium, there were 90 plant species endemic to the Centinela ridge, about 10% of the entire Centinela flora. The main ridge is now deforested, and an undetermined number of these species are now apparently extinct. Others still tenuously survive as herbs under the banana, coffee, and cacao plantations that replaced the forest, as epiphytes in cultivated trees, or on a disjunct southern spur of the ridge where we recently discovered a tiny remnant patch of forest.

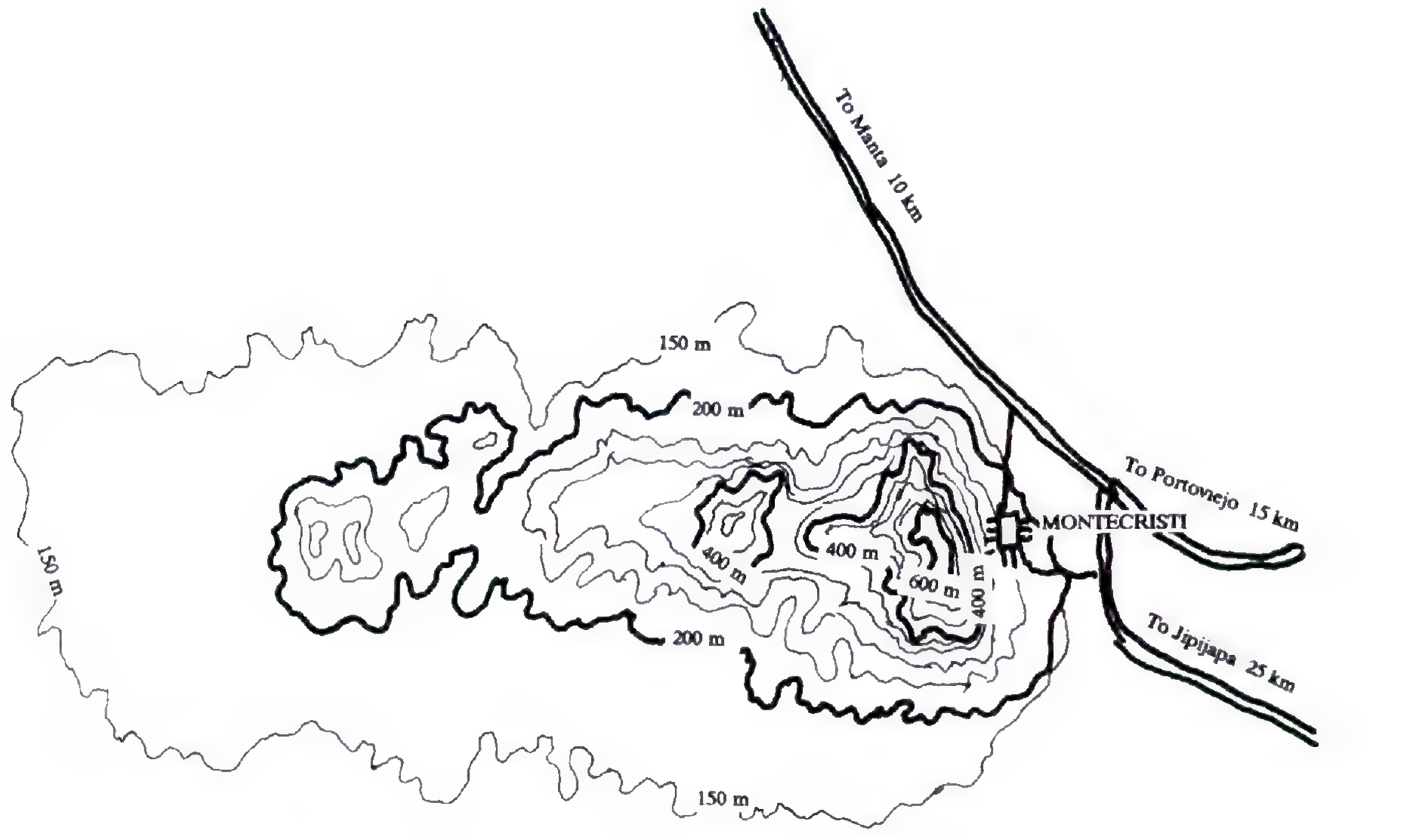
Many of the species at Centinela are strikingly beautiful and quite unlike any known congeners. One noteworthy feature shared by many species of unrelated families is that the upper surfaces of their leaves are black and usually intricately bullate.

How did so many distinctive species come to exist at Centinela? *Gasteranthus* of the Gesneriaceae provides an instructive example. This small genus of about 25 species ranges from Guatemala to Peru, mostly in cloud forests, generally with a few endemic species in each country in which it occurs. In Panama, for example, there are five species—two endemic and three shared with Costa Rica (Skog, 1978). Most *Gasteranthus* species have rather similar-looking orange flowers with a pouch-like corolla. On Centinela there are (or were) no fewer than six species, a quarter of the world total! Four of these are restricted to the high-endemism area near the southern tip of the ridge, a fifth species is also known from a single collection from north of Santo Domingo, and the sixth occurs also at Rio Palenque. Most of these six species are dramatically different from each other and from their congeners. Indeed, *Gasteranthus* shows more morphological diversity in the few square kilometers of Centinela than in the rest of its range. The endemic species of Centinela represent a high level of in situ evolution.

Our floristic knowledge is inadequate to evaluate how many isolated ridge tops shelter large numbers of endemic species as does Centinela. It is possible that many of them do (or did before being deforested). For example, preliminary observations at Lita, a high-rainfall region in Esmeraldas near the Colombian border, suggest a very distinctive flora with many species new to Ecuador and presumably to science; however, several of the putative Centinela endemics have also been discovered there. Many new and apparently endemic species are also being discovered at La Planada just across the Colombian border on a 1,700-m ridge that extends from the main Andean Cordillera (Benavides & Gentry, in prep.); at Tenefuerte, another local florula site east of Quevedo at 1,000 m, and at Cerro Azul, a 400-m ridge subject to cloud effect just north of Guayaquil.

How many such species exist and how many of them will turn out to be extreme local endemics can only be determined with far more extensive floristic data than currently available. However, we do have previously unreported data comparable to those of Centinela for a different habitat island much farther from the Andes, at Cerro Montecristi.

Cerro Montecristi, 12 km east of Manta (see Fig. 2), is one of the characteristic, outlying, isolated hills on the extreme western side of Ecuador, and provides a good example of how microhabitat fragmentation and speciation promote extreme local endemism in western Ecuador. Cerro Montecristi was explored and the flora was studied during 1957 and 1960 (Dodson & Frymire, unpublished).



CERRO MONTECRISTI

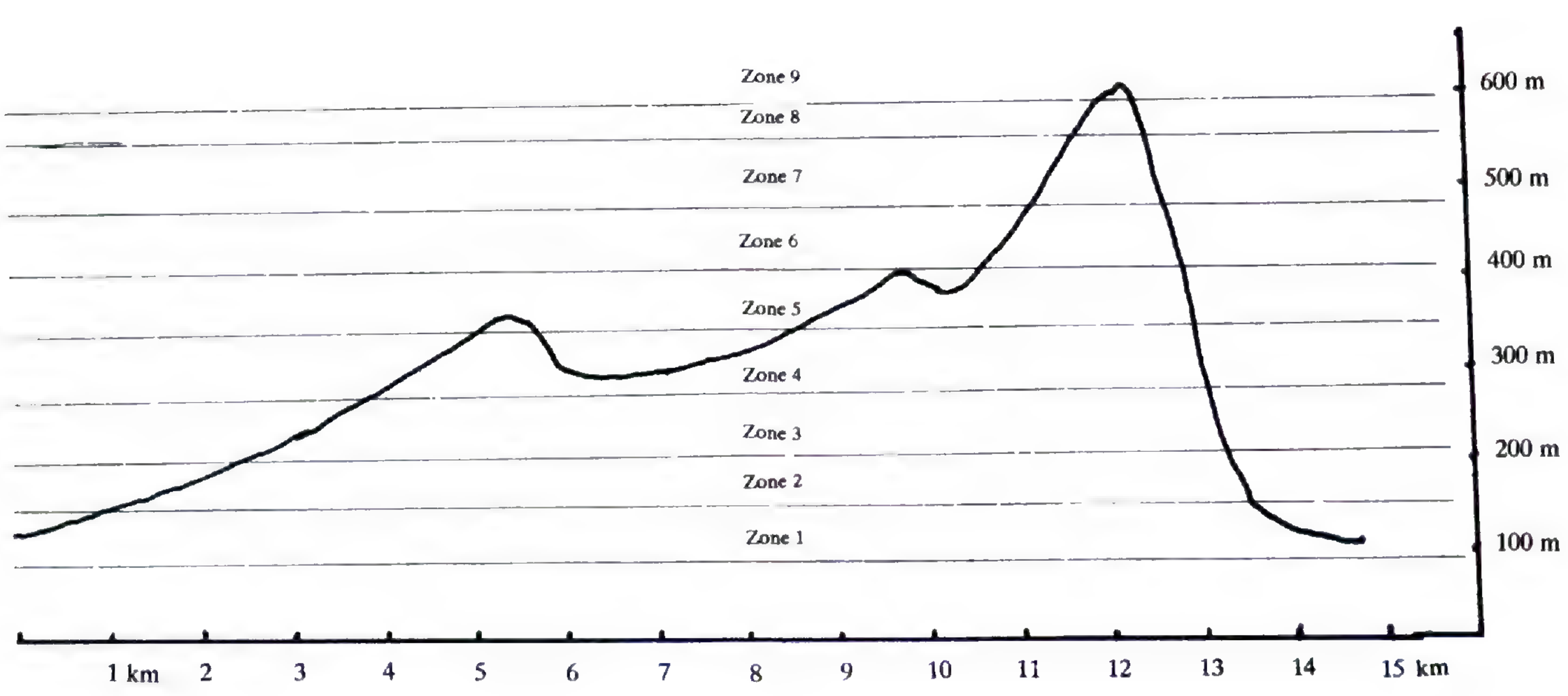


FIGURE 2. Altitudinal zonation on Cerro Montecristi.

The elevation at the base of Cerro Montecristi is about 150 m and at the summit 620 m. The hill is roughly triangular at the base and about 5 km from point to point on the eastern side with a prolonged western slope about 10 km long. The eastern face rises quite abruptly above the town of Montecristi. At night during the dry season, a cloud cover blankets the upper 100 m of Cerro Montecristi. The result is a nightly deposition of considerable moisture along the crest similar to that reported by van der Werff (1978, 1983) in the higher mountains of the Galápagos Islands. Consequently, the crest has a cover of wet-forest vegetation like those of wet forests further inland at much lower elevations. Walking from the sparse, dry scrub at the base to the summit results in crossing a sequence of habitats, each 50 to 100 m across; the lower bands are several hundred meters wide while the upper bands, on steeper slopes, are narrower. The bands probably correspond with local associations sensu Holdridge (1967). We could recognize nine distinct vegetation types.

We were particularly interested in the distribution of orchid species in the vegetation types (Table 1). Certain species were distributed through several zones, while others were limited strictly to specific zones and were encountered at the same elevation on any of the three access trails. With

the exception of zone 1, each zone has at least one orchid species restricted to it; most zones also have several species shared with other zones. Two species of orchid are known only from Cerro Montecristi, *Lepanthes manabina* Dodson and *Stelis manabina* Dodson. Both were quite common in zone 9 in a total area of probably less than 4 ha. Search of similar habitat near Jipijapa, approximately 30 km due east of Montecristi and the closest occurring vegetation of the same type, did not reveal any plants of either species.

Recent conversations with Alex Hirtz concerning the distribution of Bromeliaceae on Cerro Montecristi revealed strikingly similar distribution patterns. Hirtz is a mining engineer with a deep interest in orchids and bromeliads. He is the most knowledgeable authority on the identification and distribution of Ecuadorian Bromeliaceae. He has climbed Cerro Montecristi several times and has independently confirmed for both orchids and bromeliads the zonational distribution that we encountered in studying the orchids of the site. We have included in Table 1 the bromeliad species cited by Ing. Hirtz.

Though Cerro Montecristi may be extreme in its diversity of habitat in a very small area, like Centinela it is probably representative of the situation in much of western Ecuador. Elsewhere we have proposed (Gentry & Dodson, 1987b) that small, fragmented habitats in restricted life zones, especially in cloud forests, can promote rapid speciation, perhaps in as little as 15 years. Since the only two relatively isolated cloud forests for which we have reasonable data, Centinela and Cerro Montecristi, both show extremely localized endemism, we strongly suspect that extremely localized endemism is a common occurrence in western Ecuador. Thus, from a conservation perspective, to avoid massive extinction it is not only important to conserve patches of the major forest types, but also to conserve individual isolated or semi-isolated habitat islands.

Effects of Human Activities on the Forest Cover

HISTORICAL PERSPECTIVE

During the centuries preceding the Spanish conquest in the early 1500s, western Ecuador supported a large population of native peoples. The quantity of artifacts and ceremonial mounds scattered across the plains is so extensive that they could only have been produced by a large population over a prolonged period of time. Towns that apparently had 10,000 or more inhabitants at the time of the arrival of the conquistadores have been discovered recently in Manabi, and it has been suggested that the rural population of western Ecuador was greater at that time than it is today (P. Norton, pers. comm.). European diseases presumably drastically reduced the native population.

During the colonial period, most farming and forest conversion was restricted to the Guayas River system, the Sta. Elena Peninsula (then apparently much more humid than now according to our reading of historical records; M. Aspiazu, pers. comm.), and the seasonally dry coastal region of Manabi. The lucid descriptions of Hassaurek (1967), United States Ambassador to Ecuador from 1861 to 1866, of the region of Guayaquil and Babahoyo indicate that the population was still sparse at that time. For example, Guayaquil had an estimated population of 20,000 in 1861 vs. 1.7 million today. According to Hassaurek, most of the region from Babahoyo to the high country, even flanking the main trail to the sierra, was still unbroken forest. All available evidence suggests that substantial deforestation did not begin until after World War II, when road construction was accelerated. Figures 3 and 4 illustrate the transport system and associated deforestation of western Ecuador. Figure 3 (Map 1) shows the river system navigable by launch or canoe, the principal means of inland transport prior to roads. Figure 3 (Map 2) shows the road and railroad system existing in 1938. Because extensive deforestation seldom occurs more than 5 km on either side of a road or river bank, a combined map of roads, railroads, and river systems provides a tentative indication of where relatively undisturbed forest existed in western Ecuador prior to 1945 (Fig. 4, Map 1). At that time, we estimate that at least 75% of western Ecuador was still forested. In 1957, when the senior author first arrived in Ecuador, substantial forest conversion to banana plantations already had occurred, particularly along the post-World War II roads (Fig. 5, Map 3); however, we estimate that approximately 63% of the surface of western Ecuador still retained primary forest cover (Fig. 4, Map 2). From 1957 until 1963 the senior author was in residence in Ecuador for more than three years and spent a major portion of that time studying population distributions and pollination systems of the orchids in the forests and western Ecuador wherever roads or paths made access possible. Therefore, subsequent to 1957 we have direct evidence, albeit in part anecdotal, of the extent of deforestation in coastal Ecuador.

Between 1957 and 1988 several factors played important roles in the deforestation of western Ecuador. The population of Ecuador increased from

TABLE 1. Zones on Cerro Montecristi and their orchid and bromeliad distributions.

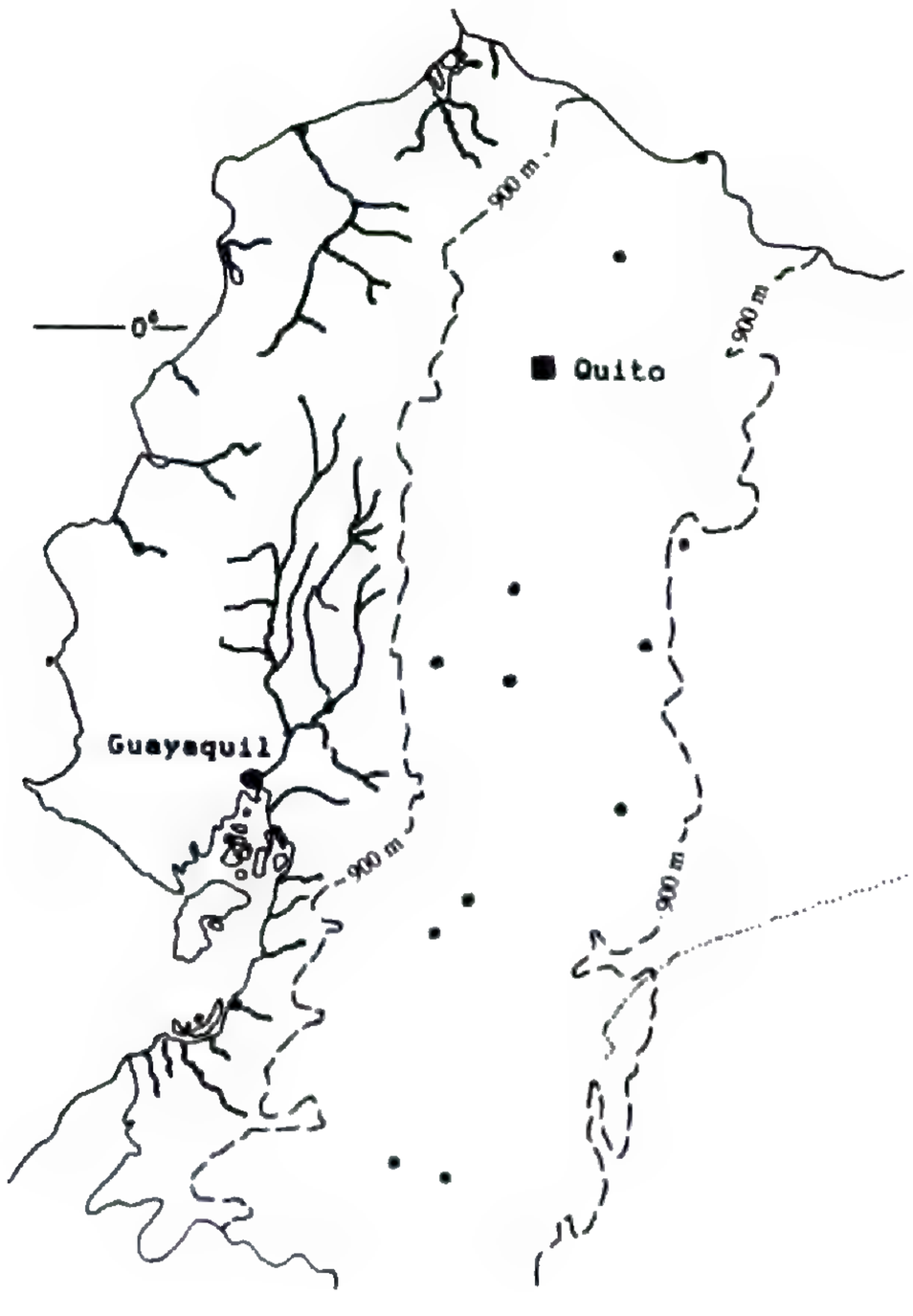
Not endemic to zone	Endemic to zone
Zone 9 600–620 m. Dominated by wet-forest elements with a dense load of epiphytes and abundant moss.	
Orchids:	
1. *Oncidium obryzatum*	1. *Dracula mopsus*
2. *Cyclopogon epiphytica*	2. *Lepanthes manabina*
3. *Masdevallia nidifica*	3. *Masdevallia zahlbruchneri*
	4. *Sobralia fenzliana*
	5. *Stanhopea frymirei*
	6. *Stelis manabina*
	7. *Pleurothallis crocodiliceps*
Bromeliads:	
	1. *Guzmannia teuscheri*
Zone 8 575–600 m. Dominated by very humid forest elements with abundant, mesic bromeliads and very little moss.	
Orchids:	
1. *Gongora grossa*	1. *Kefersteinia expansa*
2. *Ornithocephalus bryostachys*	2. *Oncidium exasperatum*
3. *Oncidium obryzatum*	
4. *Cyclopogon epiphytica*	
5. *Masdevallia nidifica*	
Bromeliads:	
1. *Guzmannia sanguinea* var. *sanguinea*	1. *Guzmannia wittmackii*
2. *Tillandsia venusta*	2. *Tillandsia hammeliana*
Zone 7 480–575 m. Dominated by humid-forest elements with mesic bromeliads and no moss.	
Orchids:	
1. *Gongora grossa*	1. *Oncidium cardiochilum*
2. *Ornithocephalus bryostachys*	
Bromeliads:	
1. *Guzmannia sanguinea* var. *sanguinea*	
2. *Tillandsia venusta*	
Zone 6 410–480 m. Dominated by dry forest mixed with humid-forest elements. Bromeliads mostly mesic.	
Orchids:	
1. *Cattleya maxima*	1. *Pleurothallis tripterantha*
2. *Trichocentrum tigrinum*	2. *Restrepia dodsonii*
3. *Gongora grossa*	
Bromeliads:	
1. *Tillandsia venusta*	
Zone 5 350–410 m. Dominated by dry-forest elements with mesic and dry bromeliads.	
Orchids:	
1. *Catasetum expansum*	1. *Campylocentrum pachyrrhizum*
2. *Cattleya maxima*	2. *Psygmorchis pusilla*
3. *Trichocentrum tigrinum*	
4. *Notylia replicata*	
Bromeliads:	
1. *Tillandsia venusta*	1. *Aechmea mexicana*
2. *Bromelia pinguin*	2. *Aechmea angustifolia*
Zone 4 280–350 m. Dominated by dry-forest elements with tillandsias as epiphytes.	
Orchids:	
1. *Catasetum expansum*	1. *Macroclinium manabinum*
2. *Cattleya maxima*	2. *Brassia jipijapensis*
3. *Trichocentrum tigrinum*	3. *Dipteranthus estradae*
4. *Notylia replicata*	

TABLE 1. Continued.

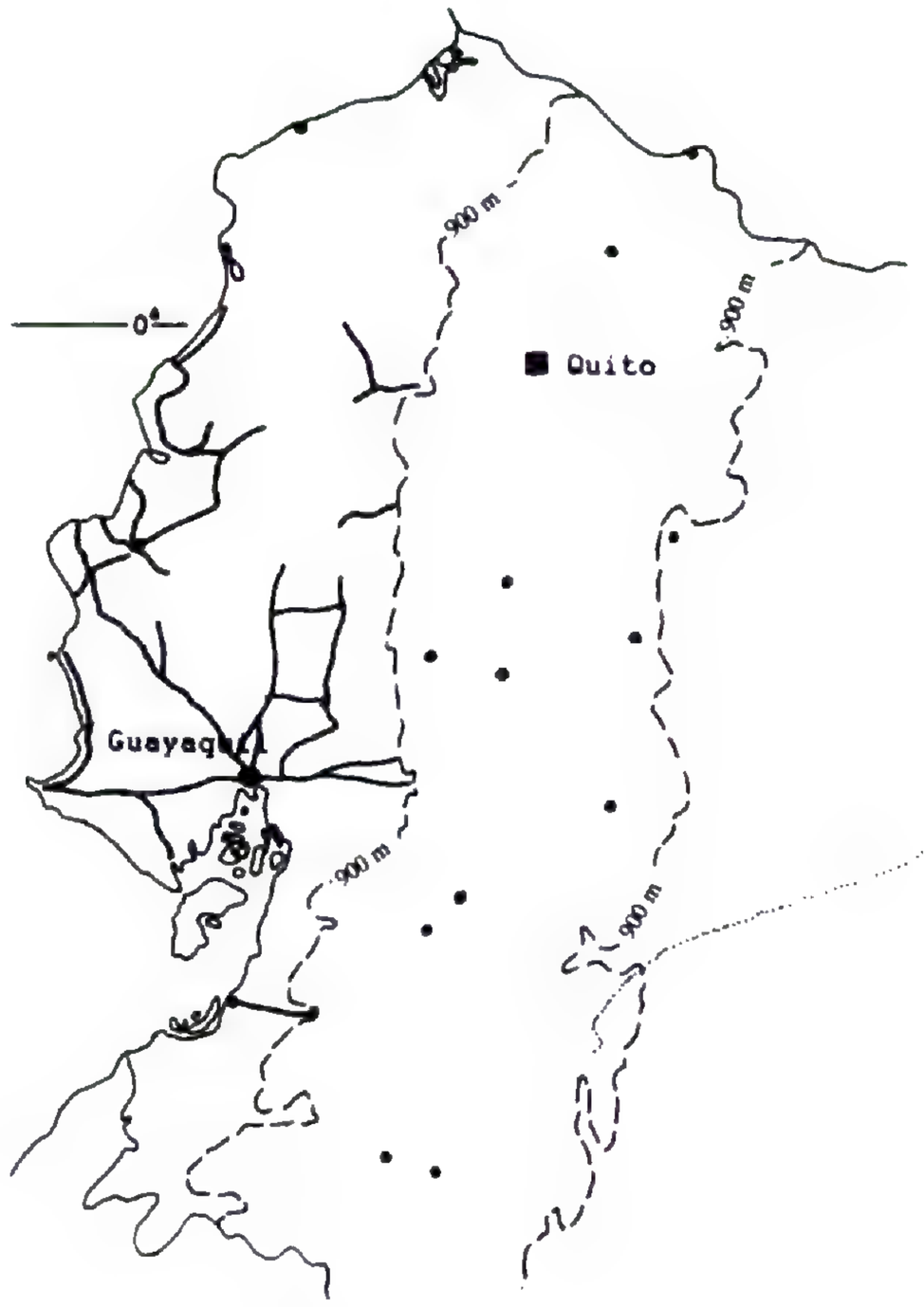
Not endemic to zone	Endemic to zone
Bromeliads:	
1. *Bromelia pinguin*	1. *Tillandsia floribunda*
2. *Vriesia barclayana* var. *minor*	2. *Tillandsia multiflora* var. *decipiens*
Zone 3 220–280 m. Dominated by very dry-forest elements and thorn forest.	
Orchids:	
1. *Catasetum expansum*	1. *Oncidium hyphaematicum*
2. *Cattleya maxima*	
3. *Trichocentrum tigrinum*	
Bromeliads:	
1. *Vriesia barclayana* var. *minor*	
2. *Vriesia espinosa*	
3. *Tillandsia multiflora* var. *multiflora*	
Zone 2 160–220 m. Dominated by thorn scrub with scattered ceibas and arborescent cacti.	
Orchids:	
1. *Catasetum expansum*	1. *Oncidium onustum* (Restricted to *Cereus* spp.)
Bromeliads:	
1. *Vriesia barclayana* var. *major*	1. *Tillandsia latifolia*
2. *Vriesia espinosa*	
3. *Tillandsia multiflora* var. *multiflora*	
Zone 1 160–220 m. Dominated by bare soil or scattered scrub.	
No orchids encountered.	
Occasional fences of *Bromelia pinguin*	

less than 4 million to 10.2 million. The natural increase rate of the population of Ecuador as of 1988 was 2.8% with a "doubling time" of 25 years (1988 World Population Data Sheet Population Reference Bureau, Washington, D.C.). Natural increase is birth rate minus death rate, implying the annual rate of population growth without regard for migration. "Doubling time" is the number of years it would take to double the population, assuming a constant rate of natural increase. This doubling time is not intended to forecast the actual doubling of a population and is simply the length of time it would take for the population to double in the absence of migration in or out, if the present birth rates and death rates continued over the next 25 years. The 2.8% increase rate is a slight decrease from the previous growth rate but is still among the highest in Latin America. In Latin America, only Guatemala, Honduras, Nicaragua, and Paraguay, all having much smaller absolute populations, have faster growth rates than Ecuador, whereas countries like Brazil (2%), Colombia (2.1%), and Peru (2.5%) have substantially lower growth rates. Land reform programs initiated in the early 1960s effectively promoted colonization of government-owned forested lands. Petroleum export provided more than 60% of the national income as Ecuador became a member of the Organization of Petroleum Exporting Countries (OPEC), selling oil at more than 35 dollars a barrel, and thereby insuring abundant new funds for development. Major sums were invested in road construction to provide communication and transport to cities and markets. Bananas, oil palm, soybeans, rice, corn, and shrimp farming, as well as the traditional cacao and coffee, became sizable export crops, providing substantial agro-industrial income. Constructed and maintained by the Ministry of Public Works, an extensive network of primary and secondary roads was developed throughout most of western Ecuador (Fig. 4, Map 4). In 1957 about 13,000 km of primary and secondary roads existed in the country (Anonymous, 1987). In 1982 (the most recent available information), there were 19,341 km of primary road and 16,276 km of secondary road for a total of 35,617 km in the Republic of Ecuador, almost triple the 1957 total. Estimates by Fausto Lafebre (pers. comm.), Director of Technical Programming of the M.O.P., indicated that as of 1987 there are more than 50,000 km of primary and secondary roads in the country, and well over half are in western Ecuador.

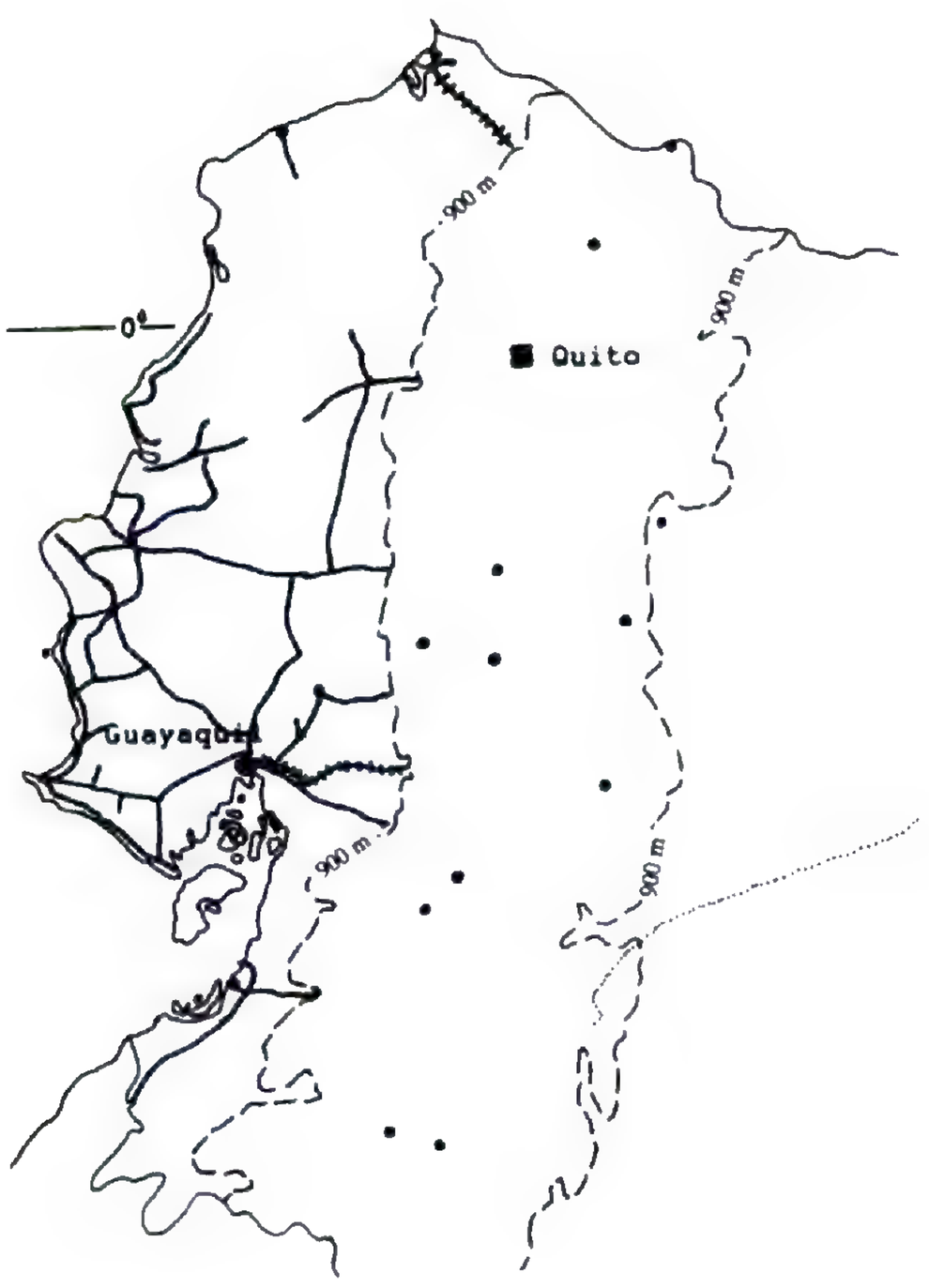
In addition, many penetration roads (or neighborhood roads, as they are often called) were con-



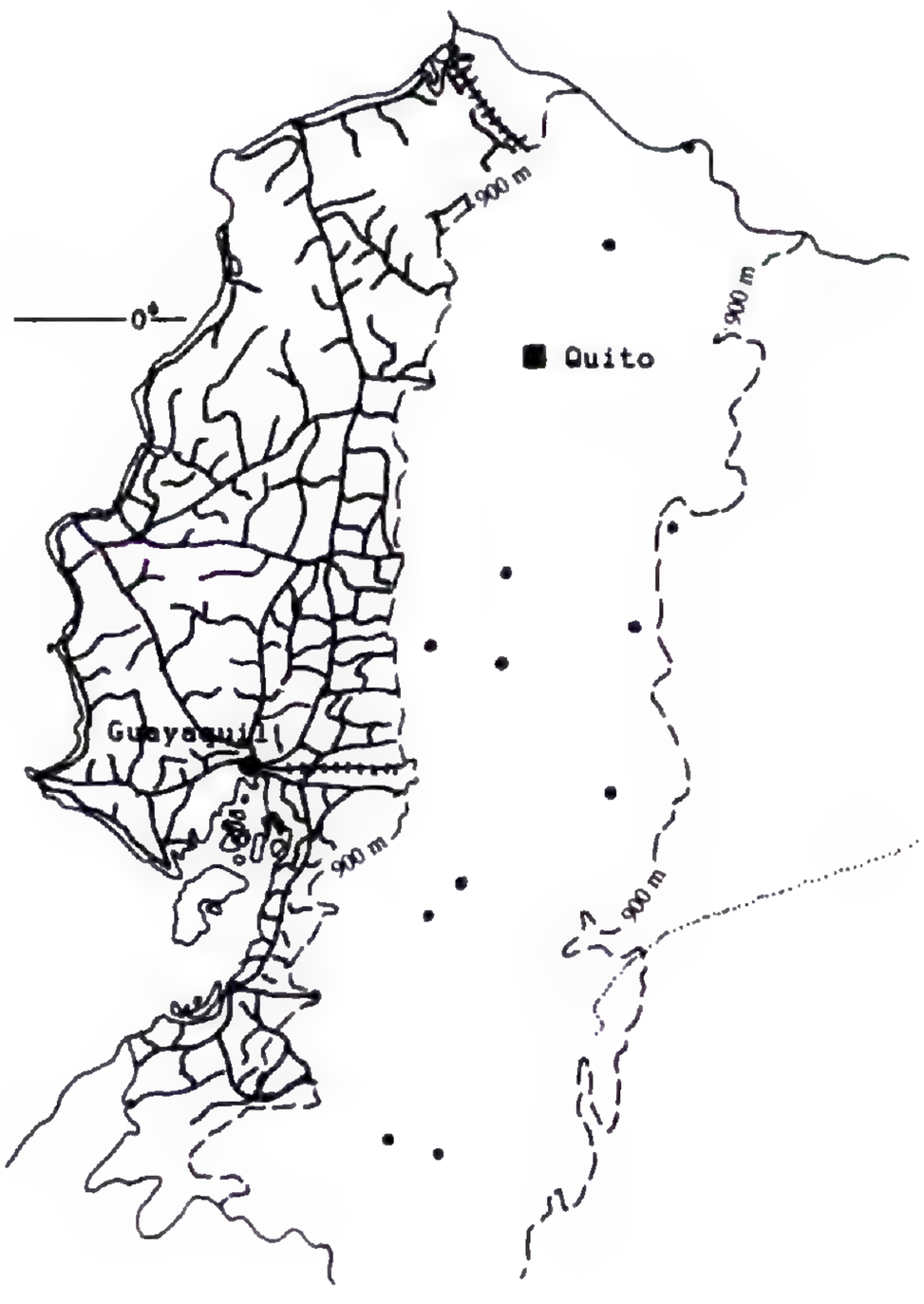
MAP 1. Navigable rivers by launch.



MAP 2. Road system 1938.

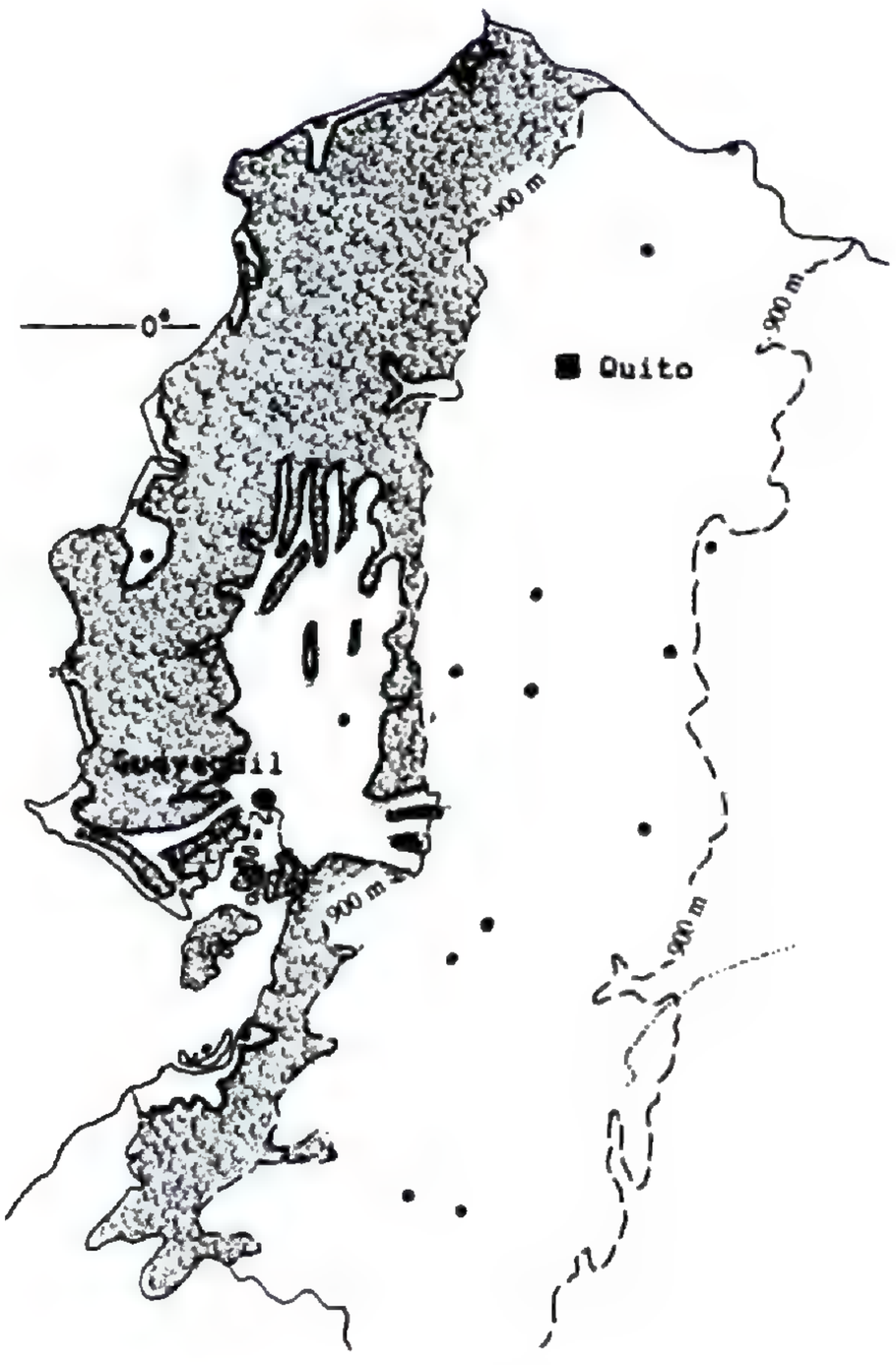


MAP 3. Road system 1958.

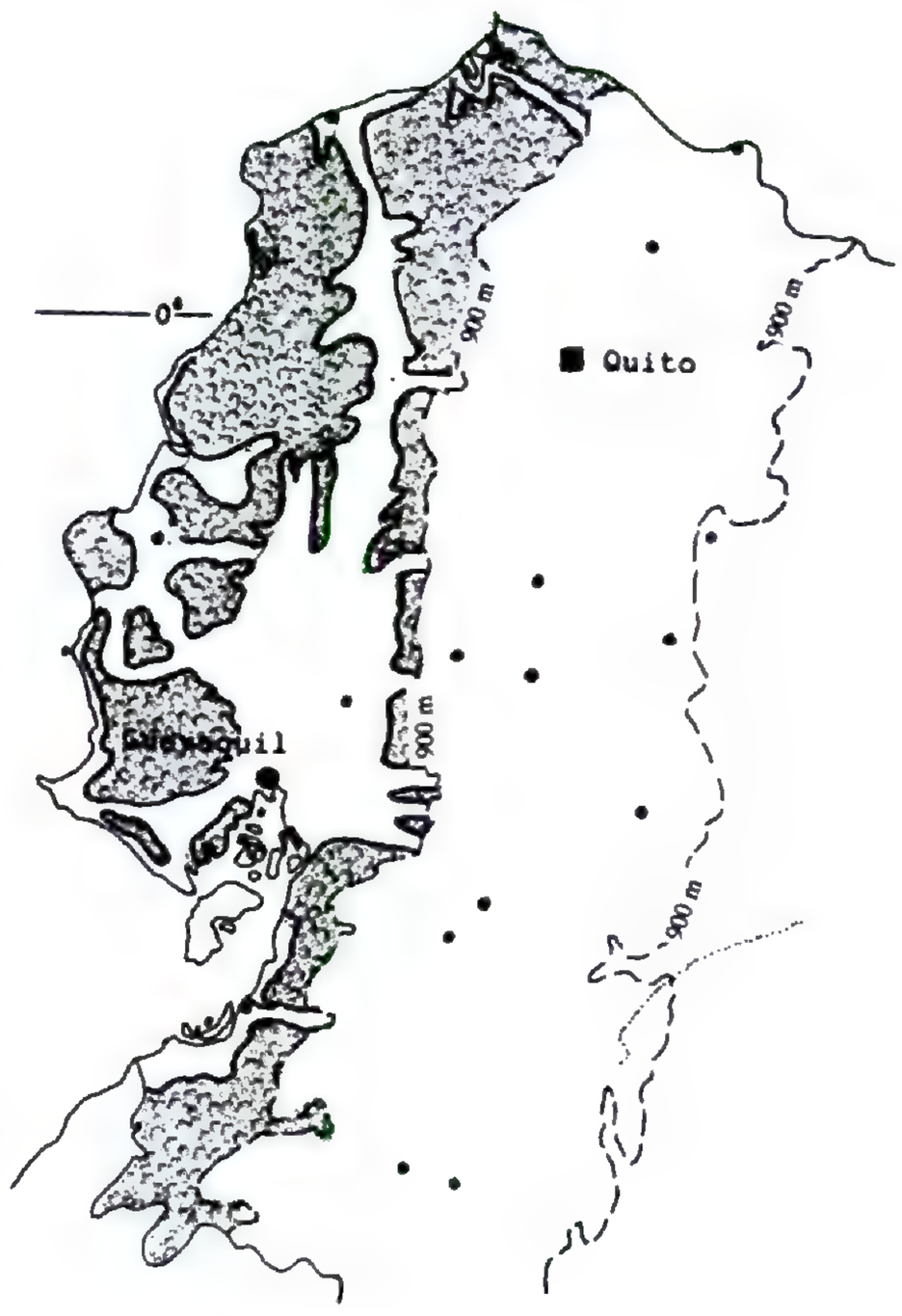


MAP 4. Road system 1988.

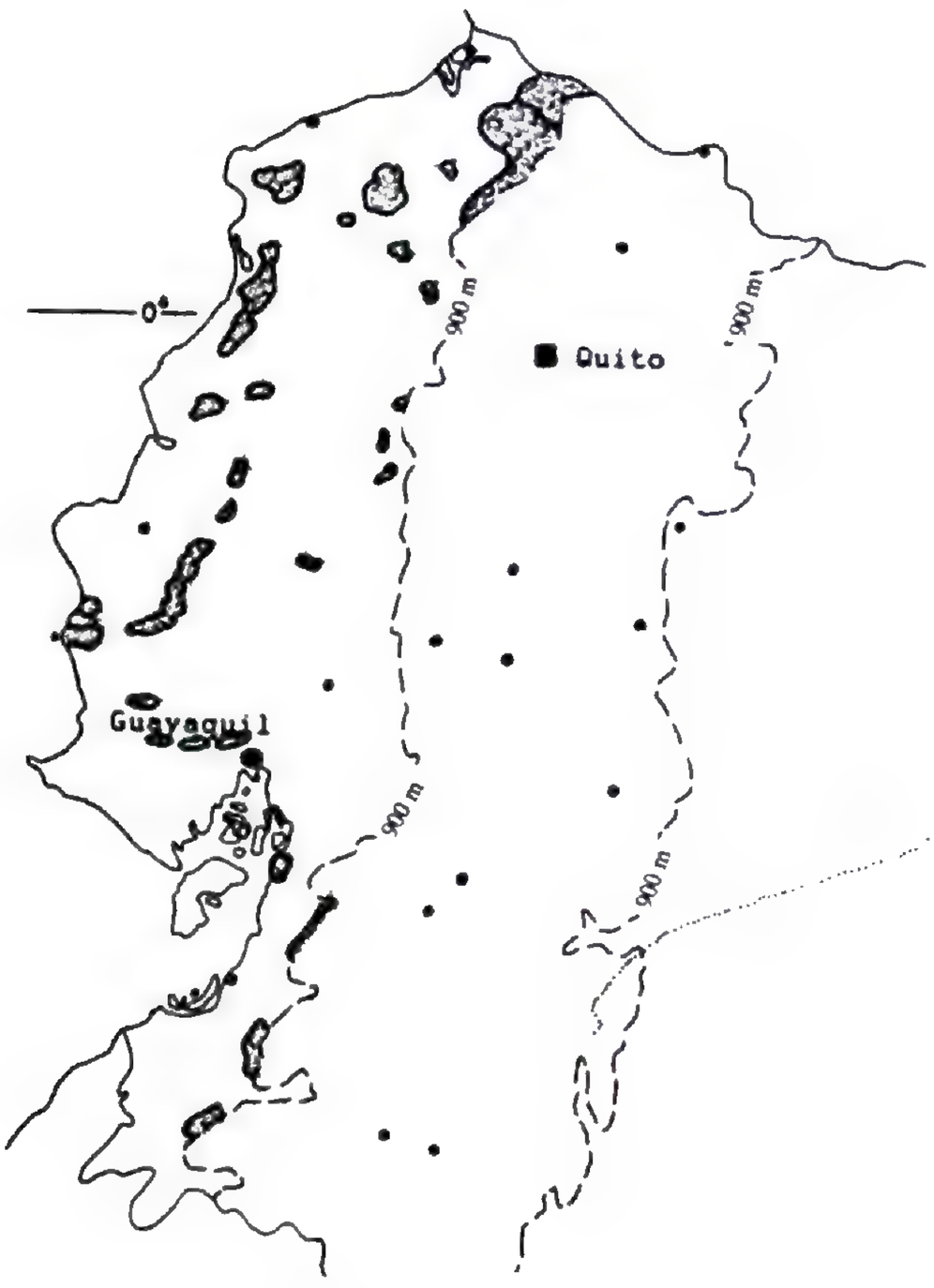
FIGURE 3. Transportation network of western Ecuador.



MAP 1. Forest cover (aboriginal).



MAP 2. Forest cover 1958.



MAP 3. Forest cover 1988.

FIGURE 4. Forests of western Ecuador from 1938 to 1988.

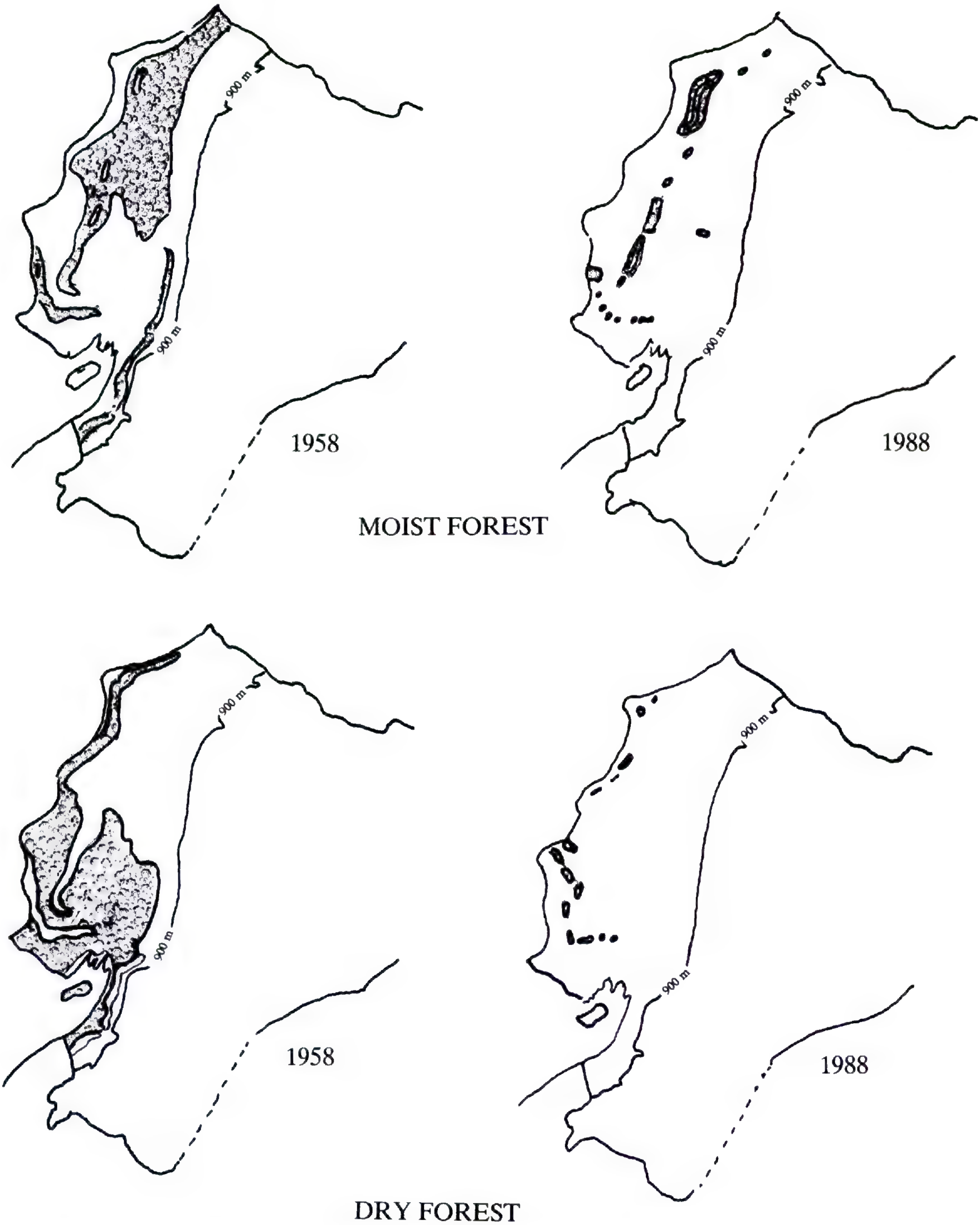


FIGURE 5. Comparison of dry and moist forest conversion between 1958 and 1988.

structed either by private enterprise or by 10–12 largely uncoordinated governmental agencies, which were programmed to help in development of agricultural colonies and cooperatives. Most of the penetration roads were constructed during the land reform efforts between 1965 and 1975 when a plan was implemented to develop and put into production all "nonproductive" lands, including all

forested lands in western Ecuador. Many of the penetration roads are not maintained by the M.O.P., and in many cases the Ministry is not even aware of their existence. No estimates of the total kilometers of these roads are available, but personal experience indicates that they are now very extensive and form a dense network that provides easy access during the dry season to all forested areas. Such easy access has had a devastating effect on the forest.

PRESENT SITUATION

Figure 4 (Map 3) displays the extent of relatively undisturbed forest known to remain in western Ecuador today. The only two substantial tracts left are in the provinces of Esmeraldas, Carchi, and Imbabura, all in the extreme north, where high monthly rainfall throughout the year has impeded development and utilization of penetration roads. These two tracts encompass the Awá Reserve (80,000 ha, with about 120,000 ha of uncommitted forest surrounding it) and the Cotacache–Cayapas Ecological Reserve (204,420 ha). More than 80% of the two tracts lies above the 900-m line outside of western Ecuador as here defined. We know from personal experience that an undetermined but clearly increasing portion of both reserves has already been cut by colonists and lumber interests. Moreover, the government is currently planning an all-weather highway that will pass through the middle of both reserves.

Much of the dry-forest reserve of the Machalilla National Park near Manta is now second growth that has been seriously disturbed by colonists and their goats. South of Guayaquil, the Churute Forest Reserve (35,000 ha) has a fairly substantial cover of somewhat disturbed mangrove but also contains disturbed dry forest on the protruding hills.

Several small private reserves exist in western Ecuador, including Capeira (10 ha) in dry forest near Guayaquil; Jauneche (130 ha) in tropical moist forest south of Quevedo; the Rio Palenque Science Center (100 ha) in tropical wet forest between Quevedo and Santo Domingo; and La Perla (30–50 ha) in premontane wet forest north of Santo Domingo near La Concordia.

Extensive mangrove forest once covered the coastal regions that were not directly facing the open sea. The advent of mariculture on a scale that provides for the largest export of shrimp of any country worldwide had reduced by 1984 the mangroves from 2,036 km^2 to less than 1,881 km^2 for a reduction of 10.6% (Alvarez et al., 1984). Considerable further conversion has taken place since 1984.

In total, we estimate that less than 5,800 km^2 of reasonably undisturbed forest remain in western Ecuador, that is, less than 8% of the land surface is presently covered by primary forest. The only two relatively large remaining forest tracts are disappearing rapidly, and construction of a new all-weather road through them will accelerate this process. The conservation picture can only be described as grim.

FOREST REMNANTS BY LIFE ZONE

Figures 5 and 6 illustrate the changes in forest cover that we have observed from 1958 to 1988 in four categories of forest: dry, moist, wet, and pluvial. These categories may each include several life zones. For example, the comparative maps of dry forest in Figure 5 encompass tropical desert scrub, tropical desert, tropical thorn scrub, premontane thorn scrub, very dry tropical forest, and premontane dry forest in the Holdridge (1967) system. All of these life zones have been severely altered by humans and by domestic animals (Table 2). We estimate that about 35% (28,000 km^2) of western Ecuador consisted of dry forest originally. Probably much less than 1% (about 200 km^2) of this category remains undisturbed.

The moist forest category, which encompasses tropical moist forest and premontane moist forest in the Holdridge system, was once the most extensive forest cover in western Ecuador (Table 2). Since the soils of western Ecuador are generally quite rich, particularly when compared with Amazonia, the moist forests were extremely attractive for agricultural development. They also have a rain-free period of at least four months, allowing easy access. We estimate that nearly 40% (32,000 km^2) of western Ecuador was covered with moist forest originally. Surely less than 4% (about 1,500 km^2) remains. Regeneration of moist forest is probably very slow, and in this case, most of the forest was clear-cut, burned, plowed, and permanently altered.

The wet forest category, encompassing tropical wet forest and premontane wet forest in the Holdridge system, was originally a band extending from Colombia to Peru. The band was about 20 km wide at the northern extreme and very narrow and broken to the south. The soils are very rich and the forests today are mostly converted to banana, African palm, and rubber cultivation. We estimate that about 15% (12,000 km^2) of western Ecuador was covered by this type of forest and that now less than 0.8% (90 km^2) survives.

Pluvial forest, encompassing premontane pluvial forest and probably lower-montane pluvial forest

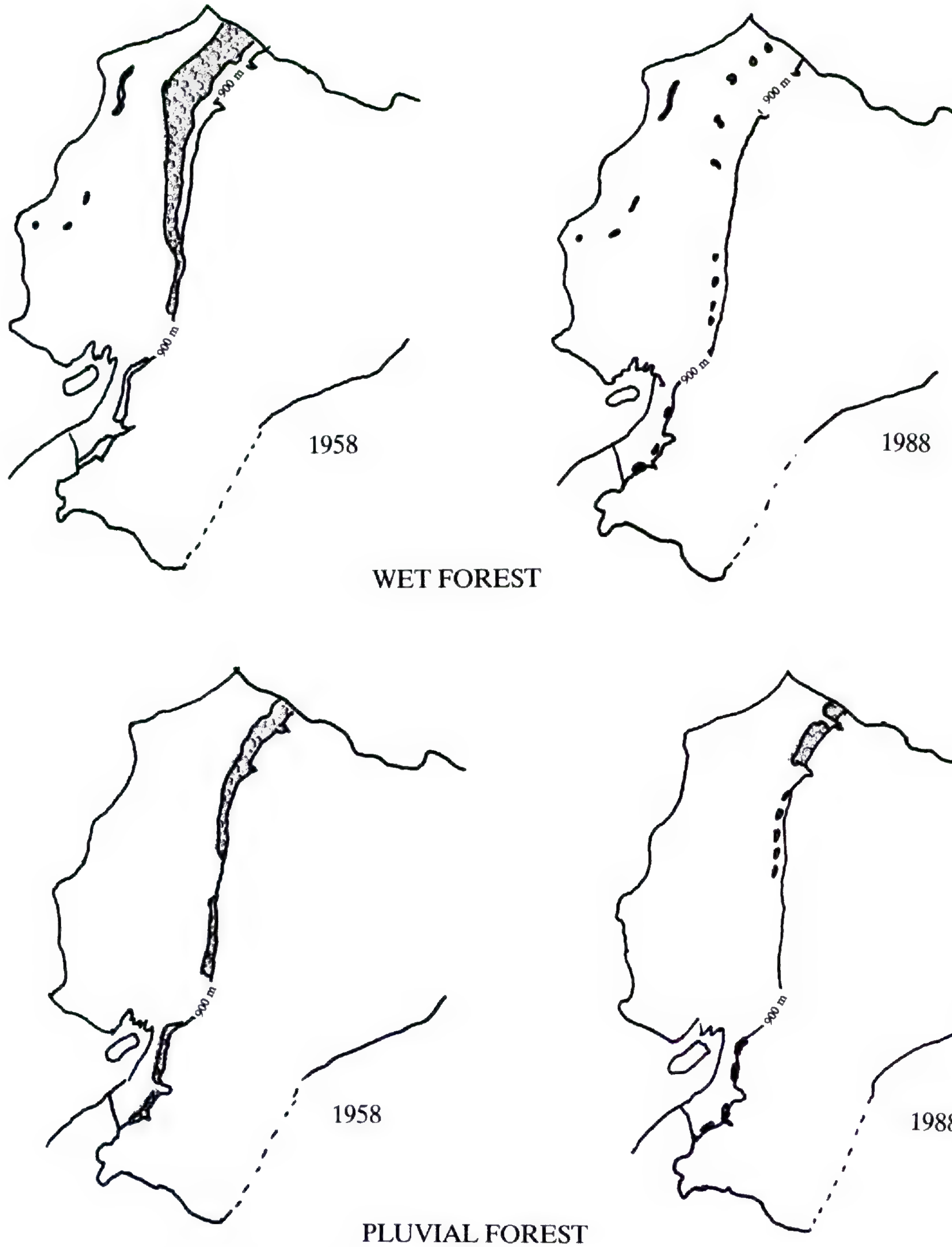


FIGURE 6. Comparison of wet and pluvial forest conversion between 1958 and 1988.

(even though the latter is not included on the Cañadas & Estrada map as known to occur in western Ecuador), forms the only substantial surviving forest category. We estimate that about 10% (8,000 km^2) of western Ecuador was covered by forests of this category and that about 25% (2,100 km^2) remains. The reasons for persistence of forest of this category are probably the notoriously poor soils resulting from leaching, inaccessibility due to high rainfall throughout the year that destroys roads that are not all-weather, and the precipitously broken nature of the terrain. These forests are of particular interest because they probably contain the highest biological diversity in western Ecuador,

TABLE 2. Areas of forest categories with estimated numbers of species and species endemic to them.

Forest categories	Original forest cover		Aboriginal forest cover		Remaining as of 1958		Remaining as of 1988		Estimated number of species	Estimated number of endemic species	%
	Km²	Total %	Km²	% left	Km²	% left	Km²	% left			
Dry	28,000	35	15,000	70	12,000	60	200	1	1,000	190	19
Moist	32,000	40	30,000	70	24,000	60	1,500	<4	1,000	140	15
Wet	12,000	15	10,000	80	7,000	58	90	<0.8	1,700	340	20
Pluvial	8,000	10	8,000	>90	6,000	75	2,100	25	2,300	590	>25
Total	80,000	100	68,000	77	49,000	63	3,890	3[1]	6,300	1,260	20

[1] This number is based on the total of 80,000 km² of western Ecuador. If the total remaining in aboriginal times is used, the remaining primary forest constitutes 4.4% of the total.

comprising part of the Chocó region (Gentry, 1982b), which contains the most diverse forests on earth (Gentry, 1986b). Though most of the still-forested lands have been declared National Ecological Reserves, they are also the only large extensions of forest left in western Ecuador in an increasingly land- and timber-starved era.

Conservation Efforts

Government-established ecological reserves and national parks

In parts of the world such as North America and Europe, an effective means of conserving forested areas is to declare them as national parks, wilderness areas, or ecological reserves. It is assumed that once so designated, previously established governmental agencies will take over management and enforcement of law. However, this assumption is not always true even in developed countries and is much less so in developing countries. More than 20% of the surface area of Ecuador has been declared to be ecological reserves and national parks. The distinction between the two is somewhat hazy, but in Ecuador only in the case of the Galápagos Islands National Park have conservation practices even approximated effectiveness. On the mainland, mining and petroleum development activities tend to take official precedence over forest preservation.

The management of national parks and ecological reserves is the responsibility of the Parks Section of the Forestry Department of the Ministry of Agriculture. The Parks Section has had good intentions and planning but is woefully understaffed and underfunded. One of the primary thrusts of the Ministry of Agriculture through its Institute for Agrarian Reform (IERAC) is "modernization of agricultural techniques and development of unused lands," while the Parks Section has as its primary but conflicting aim the preservation of those same lands. The Ministry of the Interior, with the acquiescence of the Ministry of Agriculture, gives concessions for exploratory petroleum drilling (Neill, 1988) and mining within National Park boundaries. Access roads are necessary where those activities occur. Colonists follow the bulldozers, and land titles are given to them (50 ha each). With Ecuador's burgeoning population, there seems little hope for change in political philosophy in the foreseeable future. At this time, private initiatives may be the only effective means of true forest protection.

Existence of "clandestine forest"

One of the particularly undesirable results of implementation of land reform laws enacted in the 1960s in Ecuador was their effect on privately owned forests. In an attempt to break up large land holdings, the law allowed confiscation and redistribution to landless peasants of all of the land of any hacienda that included "unproductive" land. Consequently, it became dangerous for a hacienda owner to retain natural forest on his land, since forested land was interpreted as unproductive and thus subject to seizure. The land reform act also required total conversion to production of all forest on lands deeded to colonists. As a result of this law, many haciendas in Ecuador were invaded by colonists with the support of the land reform agency. In 1971 the Rio Palenque Science Center was officially designated as a privately owned National Forest Preserve by president Jose Maria Velasco Ibarra. In 1975 an attempt was made to invade the Science Center. The 44 prospective colonists began "clearing" land in the overgrown pasture and were repelled with the help of neighboring

TABLE 3. Plant species locally extinct at RPSC.

Species	Family
Dicliptera dodsonii Wassh.	Acanthaceae
Tabebuia chrysantha (Jacq.) Nichols.	Bignoniaceae
Quararibea soegenii (Cuatrec.) Robyns & Nilsson	Bombacaceae
Pseudobombax millei (Standley) Robyns	Bombacaceae
Rohnbergia nidularioides Luther	Bromeliaceae
Tillandsia dodsonii L. B. Smith	Bromeliaceae
Burmeistera brachyandra Wimmer	Campanulaceae
Anemia phyllitidis (L.) Sw.	Fern
Gloxinia dodsonii Wiehler	Gesneriaceae
Drymonia turrialvae Hanst.	Gesneriaceae
Trichantha herthae (Mansf.) Wiehler	Gesneriaceae
Clusia venusta Little	Guttiferae
Calliandra caracasana (Jacq.) Benth.	Leguminosae
Rhynchosia precatoria (Willd.) HBK	Leguminosae
Heliconia wagneriana Wara	Musaceae
Neea ampliflora J. D. Smith	Nyctaginaceae
Elleanthus aristatus Garay	Orchidaceae
Elleanthus zamorensis Garay	Orchidaceae
Gongora grossa Rchb. f.	Orchidaceae
Leucohyle subulata (Sw.) Rchb. f.	Orchidaceae
Lockhartia serra Rchb. f.	Orchidaceae
Maxillaria alba (Hook.) Lindley	Orchidaceae
Psilotum nudum (L.) P. Beauv.	Psilotaceae
Erythrochiton giganteus Kaastra & A. Gentry	Rutaceae

farmers, resulting in no loss of mature forest (see also Gentry, 1979).

On the other hand, there are a series of laws mandating retention of limited amounts of forest, particularly along watercourses, as well as permitting governmentally protected private forests with "redeeming social value." Though a perhaps substantial number of privately owned, large farms still have appreciable amounts of natural forest, they are extremely difficult to find because the owners fear expropriation. An educated guess would be that the total of "clandestine forests" in western Ecuador might approach 100 km^2.

If one considers clandestine forests and other remnants along river courses, hilltops, and areas too broken or steep for efficient cultivation, an interrupted reticulum of existing forests still remains over a significant part of western Ecuador.

EXTINCTION EVIDENCE FROM FLORULA SITES

THE RIO PALENQUE SCIENCE CENTER (RPSC) (FIG. 7)

Extensive plant collection began at RPSC in 1973. By 1978, when the Flora was published, 1,150 species of vascular plants had been recorded (Dodson & Gentry, 1978). As of 1988, 1,294 species are known (Table 5). In 1979, ten 2 × 50-m transects, altogether totaling a 0.1-ha sample, were analyzed for woody plants > 2.5 cm dbh to quantify the structure and floristic composition of the forest (Gentry, 1982a). In 1980 a second 0.1-ha sample of the forest was conducted, this time including all vascular plants in an otherwise similar survey (Gentry & Dodson, 1987a). We have also conducted a series of phenological surveys of understory plants (Gentry & Emmons, 1987; pers. obs.). The results of these surveys provide a baseline for future comparison as well as a documentation of the relative abundance of particular species. Monthly surveys of the status of rare or more infrequently encountered species have been conducted since 1984.

Many Rio Palenque plant species are very rare or locally extinct. One species, *Dicliptera dodsonii* Wassh., known only from a single plant at Rio Palenque, disappeared in 1987 and is presumed extinct. At least 24 other species appear to be locally extinct (Table 3). Those species have apparently disappeared from RPSC but are known to occur or have occurred at other sites in western Ecuador and include a few widespread species as well as many species endemic to western Ecuador.

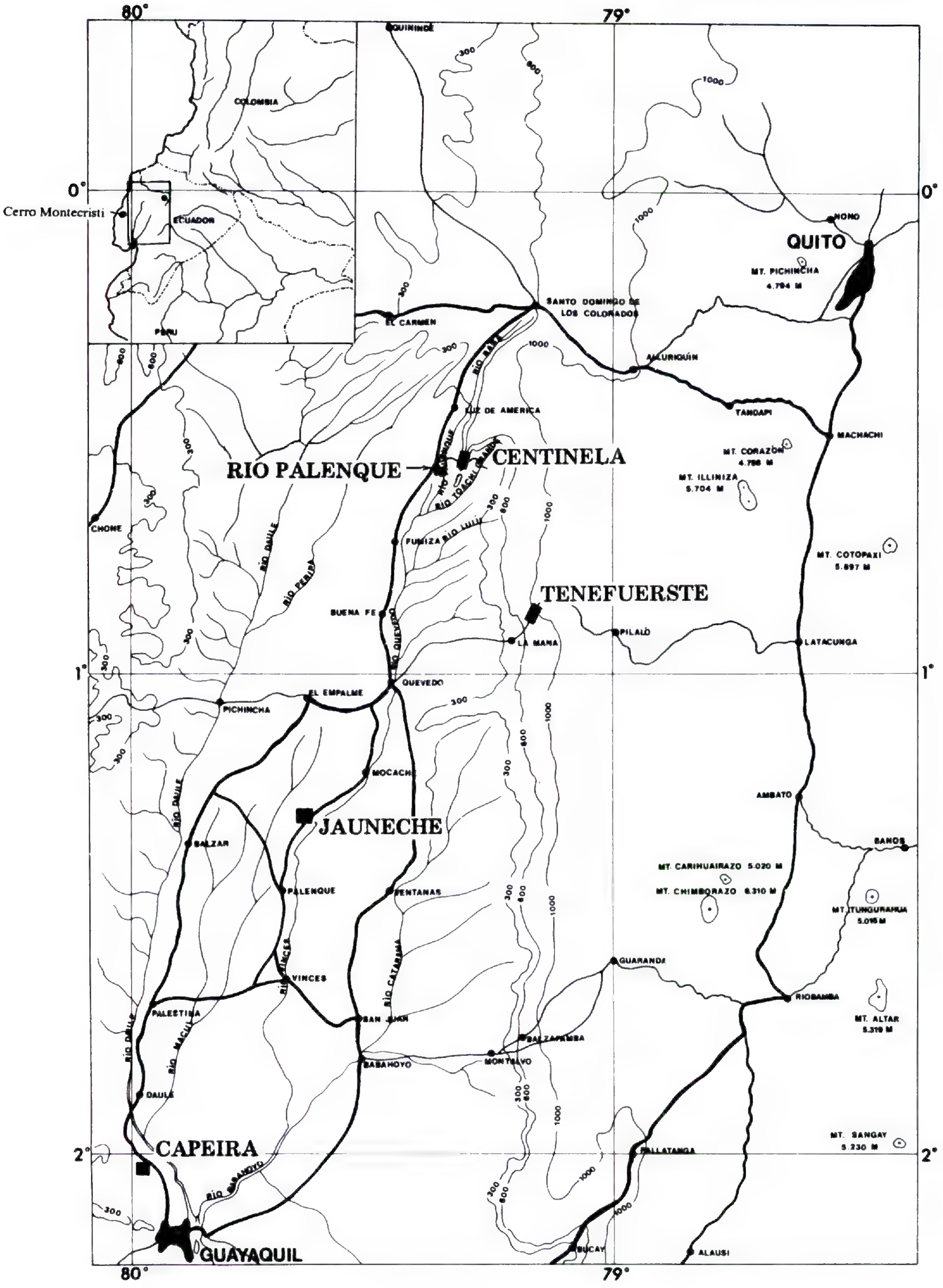


FIGURE 7. Location of field stations in western Ecuador.

TABLE 4. Plant species known from a single individual at the Rio Palenque Science Center.

Species	Family
Ocotea sodiroana Mez	Lauraceae
Bunchosia sp. (D6960)	Malpighiaceae
Trichilia septentrionalis C. DC.	Meliaceae
Epidendrum jejunum Reichb. f.	Orchidaceae
Psychopsis krameriana (Reichb. f.) H. G. Jones	Orchidaceae
Apeiba membranacea Spruce ex Benth.	Tiliaceae

Six species, mostly trees or epiphytes, are known from a single individual at RPSC. These were probably never more than accidental waifs at RPSC since substantial populations are (or were) found on the nearby Montañas de Ila or further south in drier forest (see Table 4). Another 106 species are very rare at Rio Palenque and may be in danger of local extinction. Also worth noting are 67 species now known only from Rio Palenque but with a local population sufficiently large to seem in little danger of extinction so long as the RPSC forest is preserved.

We also have relevant data on some animal groups. Since 1973 (except 1976) the senior author has taken an annual census of the euglossine bee populations at Rio Palenque. Of the potential 44 species present at the site, 32 are attracted to chemical baits (Dodson et al., 1969). Five Macphail traps are hung out for six succeeding days (usually in March) of each year, each with a different chemical bait, and the drowned bees are identified and counted at the end of each day. Fluctuations in the number and relative abundance of individual species have occurred from year to year, with one species (*Euglossa gibba* Dressler) demonstrating much greater population size during two years, but all species were still present in 1988 and in essentially the same numbers as in 1973. For butterflies, at least three brassolid species have apparently gone extinct locally but their loss may reflect replacement of their larval host, the banana plants of the prior plantation by oil palms adjacent to the RPSC forest.

In 1971 and 1982, two expeditions to RPSC led by ornithologist Oscar Owre of the University of Miami made baseline collections of birds. At that time the forests of RPSC were still connected to the extensive forests across the river leading up to Centinela on the Montañas de Ila. During the years immediately following, Richard Webster, Dan Cary, and Ken Miyata produced a local bird list of 340 species based on several months of observation. At present 355 bird species have been reported from RPSC. With the exception of three species, e.g., the Harpy Eagle, the Giant Ani, and the Long Tailed Tyrant (all of which were considered to be waifs), the resident species appear still to be present (P. Greenfield & P. Scharf, pers. comm.).

THE JAUNECHE FOREST

The Jauneche forest consists of 130 ha of tropical moist forest owned and operated by the University of Guayaquil as a biological research station. It is well protected and represents the last sizable remnant of that forest category in western Ecuador. In 1985, when the Flora was published (Dodson et al., 1985), 728 species of vascular plants were cataloged (Table 5). Transects totaling 0.1 ha were analyzed as at RPSC and compared with those of both RPSC and Capeira (Gentry & Dodson, 1987a).

Two principal types of forest exist at Jauneche. The western three-fourths of the reserve are typical upland moist forest, which once covered a substantial portion of western Ecuador. The eastern one-fourth represents a forest type, seasonally inundated, which was once extensive on the plains inland from Babahoyo and north of Guayaquil. To our knowledge this forest type has been otherwise totally eliminated in western Ecuador by conversion to rice production during the wet season, and corn or soybeans during the dry period. Several species reported by the Ruíz and Pavón expedition (probably collected by Tafalla between 1807 and 1812)

TABLE 5. Comparison of the status of vascular plant species at four sites in western Ecuador.

	RPSC	Jauneche	Capeira	Centinela
Vascular plant species reported	1,294	728	772	1,164*
Cultivated plant species	215	136	141	177
Native plants	1,079	592	631	987*
Species now extirpated at sites	25		1	84*
Remaining native plants	1,054	592	630	903*

* = Approximate due to conversion of natural forest before completion of survey.

TABLE 6. Risk situation at four sites in western Ecuador.

	Species at extreme risk due to small populations:			
	RPSC	Jauneche	Capeira	Centinela
Endemic to site	18	5	0	±84
Also found at other sites in region	49	12	18	17
Species of broad distribution	39	33	63	?
Species with short-term sustainable populations at site	942	542	559	?
Species at risk on a long-term basis	312	73	187	?
Species not at risk, primarily due to wide distribution	670	469	372	300

had never been recollected until collections for the *Flora of Jauneche* were made from 1975 to 1983. Species such as *Turnera hindsiana* Benth., *Ficus* cf. *trigonata* L. and *Pouteria* sp. (D8759) appear to be endemic to this forest and are at extreme risk.

Similarly, several species in the upland moist forest of Jauneche are presently unknown from other sites. Four of these are newly discovered species that have never been collected outside Jauneche: *Duguetia peruviana* R. E. Fries and *Annona hystricoides* A. Gentry (both Annonaceae), *Inga jaunechensis* A. Gentry (Leguminosae), and *Aspidospermum jaunechense* A. Gentry (Apocynaceae). Others, such as *Erythrochiton carinatus* Little (Rutaceae), *Erythroxylum patens* Ruiz ex O. Schulz (Erythroxylaceae), and *Aspidospermum myristicifolium* (Markgraf) Woodson (Apocynaceae), are local endemics in western Ecuador and probably now only occur at Jauneche. Most of these species, with the exception of *Annona hystricoides*, seem to have substantial populations at Jauneche and are not at immediate peril as long as the forest remains intact.

Fewer data are available than at RPSC but Tables 5 and 6 provide information on the status of the flora.

CAPEIRA

The forest reserve at Capeira consists of 10 ha of somewhat disturbed tropical dry forest owned at present by the Capeira Corporation but being operated by the Fundación Natura office in Guayaquil. It is anticipated that permanent protection by transfer of title to Fundación Natura will be accomplished soon. Transects surveyed at Capeira as part of the Flora preparation and published in the *Flora of Jauneche* (1986) make comparison with RPSC possible (Table 5). The area surveyed is on the slopes of low hills (crest at 220 m) in tropical dry forest with possible premontane dry forest elements.

The most striking feature of the dry forest near Guayaquil is its explosive exuberance of vegetation at the beginning of the rainy season in late December or early January. During the dry period, from May through the end of December, the vegetation consists of deciduous trees and brown dried leaves of the herbaceous plants and vines. Massive flowering of trees and perennial vines occurs in December and early January, while annuals and shrubs tend to flower from March through April. Sporadic flowering occurs during the dry season. Selective logging of highly valuable hardwood trees such as *Tabebuia chysantha* (Jacq.) Nichols., *Tabebuia billbergii* (Bur. & Schum.) Standley (both Bignoniaceae), *Alseis eggersii* Standley (Rubiaceae), and *Myroxylon balsamum* (Leguminosae) has put those trees at risk locally, but their broad distributions throughout the dry forest remnants of the coast suggest that they may be salvageable. Only one new species, *Prockia pentamera* A. Gentry, represented by a single individual (now deceased), was discovered at Capeira; this species has since been discovered in the Cerros de Amotope on the Peru–Ecuador border (Gentry, 1988).

THE FORESTS OF CENTINELA

Centinela was a florula site consisting of about 100 ha, located along the ridge line at the southern extreme of the Montañas de Ila, about 12 km directly east of RPSC. Most of the site is at elevations from 550 to 650 m. The forest cover of the entire length of the Montañas de Ila, from Santo Domingo to Centinela, has now been converted to pasture, coffee, or cacao. A few remnants still exist in ravines and areas too steep to cultivate.

When collections began at Centinela in 1975 there seemed little reason for concern because the Montañas de Ila were essentially untouched. We were becoming uneasy by 1980 when preparation of the florula began, and by 1985 we were alarmed. By 1988, the site of Centinela had been completely converted from forest to agriculture. The flora of Centinela was extremely diverse, particularly in epiphytes and understory shrubs and herbs (Table

5). Although approximately 48% of the naturally occurring species at Centinela were shared with RPSC, about 10% of the flora appeared to be strictly endemic to the site (see Gentry, 1986a).

Comparison of the floral composition of Centinela with that of the area between Lita and Alto Tambo in the province of Esmeraldas near the Colombian border indicates that the forests of Centinela were premontane pluvial on the Holdridge system. Approximately 80% of the species are shared with Lita, and some species extremely rare at Centinela are common at Lita. We had assumed that most of the nearly 100 species endemic to Centinela became extinct when the forest was cut. This conclusion was supported by failure to locate these species in similar habitats north of Santo Domingo. However, in only five relatively short visits to Lita we have now found 11 species that we had considered to be extinct at Centinela (plus several additional new species). Another site at Poza Honda near La Mana in the province of Cotopaxi east of Quevedo, about 70 km due south by air from Centinela, has been found to have six species of those previously considered to be extinct at Centinela. Probably others remain to be found, since we have only made one visit; however, this site is also threatened, so their discovery at Poza Honda is likely only a short reprieve. Nearly all of the refound Centinela plants were epiphytes or understory herbs. On the other hand, further study of the Centinela herbarium collections continues to add additional new, perhaps already extinct, local endemics that were not included on our original list, more or less balancing the "lost" endemics.

Many epiphytic plants and understory herbs at Centinela have survived in the cultivated orchards that replaced the forest. We first encountered this phenomenon at Jauneche where 63 species of epiphytes were found. Transect studies in the forest indicated population density to be very low (Gentry & Dodson, 1987b), whereas in a nearby cacao orchard most of the same species (and seven species that were not encountered in the forest) were nearly an order of magnitude more dense (Dodson, unpublished). At Centinela we now find many of the extremely threatened epiphytes forming substantial populations in cacao trees and shade trees for coffee. Even *Epidendrum ilense* Dodson, which had been given up as extinct in the wild (Dodson, 1981), has been recently encountered as a substantial population in a 13-year-old cacao plantation at Centinela.

In summary, we do not know how many endemic species have already gone extinct on Centinela; all are in dire peril. Although all or most of the trees that were endemic to Centinela may already be extinct—e.g., *Carapa megistocarpa* A. Gentry (Meliaceae), *Brownea* n. sp. (D6846) (Leguminosae), and the shrubby tree *Erythrochiton giganteus* Kaastra & A. Gentry (Rutaceae)—many of the herbs and epiphytes have thus far survived. Discovery of several of the Centinela "endemics" at two additional recently explored sites would somewhat lower our estimate of the original level of endemism on the ridge, but several additional new species have also been recognized. The only solid conclusion may be that we still know so extremely little about the plants of western Ecuador and their distributions that we cannot hope to make educated conservational decisions without a far more extensive floristic data base.

Natural and Man-made Fragmentation

Western Ecuador has an extremely diverse flora. As indicated above, we estimate that there are more than 6,300 species in an area of 80,000 km^2. A substantial portion of the diversity found in western Ecuador is probably part of the general syndrome of explosive speciation in the northern Andes (Gentry, 1982a; Gentry & Dodson, 1987b). The causal mechanisms for that explosive speciation are not well understood, but surely one of the factors is the plethora of microhabitats in the region. Not only are there a large number of microhabitats in western Ecuador, but they are spatially isolated due to the natural fragmentation of many of the life zones. Of the 12 or 13 life zones, eight to ten often were represented, even originally, by small to very small, largely noncontiguous patches of forest strung out in a linear fashion either along the tops of the coastal mountains or the lower slopes of the Andes. It is in those natural fragments that speciation was presumably most rapid, judging by today's exceptionally high endemism.

The forest fragments that now remain after humans have essentially obliterated the forest over the majority of western Ecuador tend to be in the most inaccessible areas. They often are located near the summits of the coastal mountains or along the steep flanks of the Andes. These tend to be humid- to wet-forest fragments with high species diversity and high natural endemism, including some of the "clandestine" forest reserves mentioned above.

We suspect that much of the flora of western Ecuador is based on a different set of evolutionary parameters from that of large expanses of relatively homogeneous tropical zone habitats. These include extremely rapid speciation, adaptation to survival with very low population densities, adaptation to

small habitat patches, and perhaps concurrent rapid natural extinction rates. Thus, we would submit that conservation of even the tiny habitat fragments that remain in western Ecuador might well conserve a substantial portion of the estimated original complement of 1,260 species endemic to the area, despite the tremendous deforestation that has taken place. Any such effort must be undertaken very soon, however, since no matter how adept at surviving in habitat fragments many of these species may be, they will surely all be lost if the few tiny forest patches that remain today are lost.

Synopsis of Data and Discussion

1. The forest cover of a significant but indeterminate part of western Ecuador had already been somewhat altered prior to the time of the Spanish conquest, perhaps as much as 30%. The catastrophic effect of European diseases apparently reduced the indigenous population drastically, and much natural reforestation occurred before the beginning of the twentieth century.

2. At the end of the nineteenth century most of western Ecuador was covered by intact forest (at least 75%) except for regions easily accessible by boat along the rivers.

3. Most forest conversion in western Ecuador occurred between 1960 and 1980, principally as a result of road construction and demographic explosion; today, approximately 4.4% of the aboriginal primary forest cover remains. The moist- and wet-forest categories were most severely reduced, from 50% to less than 1% and from 15% to 0.1%, respectively.

4. The population of Ecuador is increasing at an alarming rate that shows little indication of slowing. The present population is more than twice that of 1957 and doubling of the 1988 (10.2 million) population is expected by the year 2020. The need for resources to support that population will make for even greater pressure for conversion of natural forests.

5. Western Ecuador was very diverse ecologically with 12 or 13 Holdridge life zones in 80,000 km^2. The forests of most of those life zones were distributed in long narrow bands or scattered through the coastal mountains.

6. Considerable local endemism occurred in each life zone, at least partially due to their long, narrow forms and natural fragmentation.

7. Extrapolation from florula data indicates that the flora of lowland western Ecuador probably contained about 6,300 species of vascular plants. We estimate that about 1,260 of these are endemic to this region.

8. Island biogeographical theory suggests that the drastic eradication of habitat during the last two decades should have resulted in substantial extinction by now, but the baseline floristic data are insufficient to know whether this has happened.

9. Florula data suggest that very many species, about 4% of the florula floras, are at extreme risk at this moment. We estimate that perhaps 12% of the flora of western Ecuador is at risk in the near future. Many species have very precariously survived partially because of a network of minute patches of private, in part clandestine, forest reserves.

10. With the exception of the two threatened forest reserves at the northern extreme (only 80 km^2 of which lies within western Ecuador as here defined), very little natural forest remains in western Ecuador—ca. 4,000 km^2 or 4.4% of the aboriginal total of 77% of western Ecuador.

11. Federal protection of established national parks and reserves is inadequate.

12. Demographic pressures and political realities project a very grim future for effective conservation of what remains unless immediate steps are taken.

13. Unless adequate protection is given to the remaining forest fragments, including the tiny private reserves in the south as well as the two larger ones in the north, a major extinction of perhaps 1,260 endemic plant species can be expected in western Ecuador in the very near future.

14. Unlike Amazonia, the soils of much of western Ecuador tend to be rich and if well managed will sustain agriculture for an indefinite period; therefore, conservational decisions must be based on the comparative values of conservation of forests versus the land's potential value when placed in agricultural production.

What Can Be Done?

Though the conservation scenario in western Ecuador appears to be very grim, we feel that several actions could be taken to save a portion of the remaining diversity of plants and animals. As indicated above, western Ecuador is very diverse biotically with 12 to 13 Holdridge life zones. Small portions of each of those life zones still exist as private reserves, clandestine forests, or federal reserves. We suggest that if even the tiny extant fragments can be effectively preserved there may yet be reason for optimism of preserving a portion of western Ecuador's ca. 1,260 endemic species, especially in view of apparent adaptation of many of these endemic species to an originally small and fragmented habitat.

ACTIONS THAT MIGHT HELP TO SAVE THE REMAINING DIVERSITY:

a. Strengthening of federal efforts through private institutions.

Governmental efforts to preserve forests that have been declared to be reserves or national parks have had a dismal record of success in Ecuador except in the Galápagos Islands. Until recent times there has been little external or internal interest in conservation in mainland Ecuador.

The development of private, conservation-oriented Ecuadorian foundations within the last decade, such as Fundación Natura, dedicated to conservation principles and with surprising internal support, holds hope for a major change in direction. Those foundations have been spectacularly successful in modifying popular opinion in the country and are making strides in changing attitudes of governmental agencies. A program of support of natural history education at the elementary school level, daily articles in the newspapers, establishment of the Pasachoa Nature Reserve by Fundación Natura, and ecological activism on all fronts may play an important role in changing conservation practices in the country.

b. International pressure to save the Awá and Cotacachi–Cayapas reserves.

If the Awá and Cotacachi–Cayapas reserves are to be saved for posterity a major effort must occur soon. Plans exist to construct roads that will open the two areas to colonization. A substantial portion of the biological diversity in western Ecuador still persists within those two preserves. They are still of sufficient size that all resident flora and fauna can persist. However, without those preserves massive extinction will surely occur.

International attention to the plight of the two reserves must be brought to bear now. Though the Galápagos are world renowned, have many endemics, and spectacular tourism impact, the two reserves have much greater diversity, far more endemics, and extreme potential impact from extinction. The two reserves have an astounding diversity and much of it is endemic; the 1,260 endemic species of western Ecuador are nearly twice the total flora of the Galápagos. Even the forests of the 1 km² Rio Palenque Science Center have nearly twice as many species of vascular plants as all of the Galápagos Islands, and the nearly 100 endemic species of the 20 km² Centinela Ridge are nearly half the total of endemics that occur on the Galápagos.

c. Survey of remnants and development of small nurseries at established sites for plant species at extreme risk.

It is important that survey and identification of forest remnants and fragments be accomplished as soon as possible. This can be done by use of satellite imagery and overflights. Once located, the fragments must be explored to determine preservational status of the forest and the presence of endemics. When the endemics are discovered, their population status must be ascertained. The important forest fragments should be protected as forest reserves. Species at extreme risk could be propagated in small, relatively unsophisticated nurseries in similar habitats and reintroduced as necessary. In addition, seeds can be collected for preservation of genotypes in seed banks.

Nurseries can be developed at already established sites with a minimum of expense. For example, nearly all of the dry-forest species could be maintained at Capeira with minimum care. Moist-forest species can be grown at Jauneche, and wet- or pluvial-forest species at RPSC.

Update on Status of Forests of Western Ecuador
(10 Feb. 1991)

In 1990, Luis Mejia of the Ministry of Agriculture (MAG) prepared an unpublished report similar to this one for Fundación Natura, based on Landsat photos taken between February 1985 and February 1989. Accompanying that report is a detailed map showing forest types and extent. Mejia demonstrates that we were not only correct in our assessment but were even overly optimistic. Mejia's study area was much larger, including all of the western slope of the Andes and totaling 102,000 km², whereas we only used up to the 900-m line, and included 80,000 km². Mejia indicates 15.4% of western Ecuador still in primary forest. The fundamental difference in the two studies is that the northern portion of the area above the 900-m level contains the major portion of the 3,000 km² of the Cotacachi-Cayapas and the Awa reserves, which are mostly in primary forest. Other existing forests not considered by us are at elevations higher than 900 m in Imbabura and northwest Pichincha provinces. Consequently, even less than the 4.4% of lowland western Ecuador, still in primary forest predicted by us, existed at the time of the study by Mejia. Of particular note, Mejia's map indicates that only one block of primary moist or wet forest exists south of Santo Domingo. That block lies just west of Volcán Corazón at elevations between 2,000 and 3,000 m. No others occur in the lower two-thirds of western Ecuador. Mejia also demonstrated that of the 102,000 km² of western Ecuador, 15,744 km² of primary forest exist, but only 22,000 km² have forest of any sort. During the 2 to 3 years since the Landsat photos were taken deforestation has accelerated. Only the northern reserves and the Chindul mountains in

extreme western Manabi and Esmeraldas provinces remain forested, and even there the chain saws drown out all other sound from dawn to dusk.

If all of western Ecuador is considered (as did Mejia) using the same criteria (based on the relatively well known orchid data for the region—1,303 orchid species with 447 endemic species) for predicting species content as we did, then 13,000 species of flowering plants occur in western Ecuador, including more than 3,000 endemic species.

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STUDIES OF ANGIOSPERM PHYLOGENY USING PROTEIN SEQUENCES[1]

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ABSTRACT

In previous papers we have reported the N-terminal 40 amino acids of the small subunit of rubisco for samples from four families of gymnosperms, nine families of monocotyledons, and 26 families of dicotyledons. We expanded this list to 122 families of dicots and derived a phylogenetic tree for all 335 species. The main computing program used was HENNIG86, with which a reliable result can be assured with only 17 taxa or less, so a major part of this paper is concerned with the strategy adopted to divide the 335 species and then to build the parts into an overall tree that is as accurate and objective as possible. Comparison with other taxonomy suggests that, at the level of placing genera into families, our methods give results that are at least 90% accurate. At higher taxonomic levels accuracy may decrease, and the result should be regarded not as a firm conclusion but as a working hypothesis for subsequent testing using the longer sequences from nucleic acids. Topics discussed include heterogeneity within species, the nature of the N-terminus of rubisco-SSU, and evidence that natural selection is powerful in determining amino acid sequence. The rate of evolution has been shown to vary between major taxa, and data suggest that angiosperms originated in the Jurassic.

The problems of angiosperm phylogeny are well illustrated by a consideration of the differences between four classifications, all less than a decade old and all by highly respected and experienced authors. The dicotyledons are divided into six subclasses by Cronquist (1981) and seven by Takhtajan (1983), while, for the other two authors, the major groupings are superorders, Thorne (1983) having 19 and Dahlgren (1983) 25. The number of dicotyledonous orders recognized is, respectively, 58, 72, 41, and 83; these figures alone indicate the resulting diversities of names and content, all of which reflect our comparative ignorance of the course that evolution has taken in the angiosperms. In contrast to this, at the next level down the hierarchy, there is basic agreement about the "core" families to be recognized (Heywood, 1978).

Macromolecular sequences provide taxonomic characters whose homology over widely diverse species can be assumed with some confidence. Sequence data can be analyzed objectively with computers. We will probably see in the next decade the publication of nucleic acid sequences long and variable enough to solve some of the problems of angiosperm phylogeny (e.g., Palmer et al., 1988; Zimmer et al., 1989). It is therefore an appropriate time, when nucleic acid sequencing is supplanting protein sequencing, to set out the results of a decade of work that has produced 335 partial protein sequences from a wide range of angiosperms. These sequences are shorter than nucleic acid sequences already published and therefore contain less information and are less able to resolve the sequential divergences of early radiations. Nevertheless, we believe that our phylogenetic trees will indicate likely relationships and profitable working hypotheses for future investigations.

A SUMMARY OF PUBLISHED INVESTIGATIONS USING PROTEIN SEQUENCES

The pioneer of the use in botany of protein sequences for investigating plant phylogeny was D. Boulter of the University of Durham, England. During the 1970s, Boulter, along with his colleagues and students, published 25 sequences of cytochrome c, 12 complete and 58 partial sequences of plastocyanin and seven sequences of

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ferrodoxin. These have been collated, with references, by Ramshaw (1982), and Scogin (1981) has reviewed the results from the taxonomic point of view. Although this work generated much interest, it also gave rise to skepticism, some of which can, with hindsight, be attributed to the inadequacies of computing methods that were being developed concurrently. The mostly unfavorable reaction of systematists, epitomized by the review of Cronquist (1976), influenced the cessation of research in Boulter's laboratory about 1980.

Before this, however, partial sequences (up to 25 N-terminal amino acids) of the small subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco-SSU) were obtained from six species (Haslett et al., 1976; Strobaek et al., 1976). This work led to a complete SSU sequence from spinach (Martin, 1979), a forerunner of the work presented here which concerns the N-terminal 40 amino acids of this protein. (The complete sequencing of a protein requires prior purification of several fragments and is at least an order of magnitude more time-consuming than the direct sequencing of the N-terminus of the whole protein using an automatic sequencer.) Nucleotide sequences of rubisco-SSU from a few species have been published, and all of them have been studied using our method. The only new data comparable to our 334 species are from two closely related orchids and their hybrid (G. C. Martin et al., 1987). We are unaware of phylogenetically useful sequences of other proteins since those of Grund et al. (1981) and Nakano et al. (1981).

Work in our laboratory has proceeded in five phases. In phase 1 species were chosen because Boulter had already published their complete sequences of cytochrome c and partial sequences of plastocyanin. When a pattern failed to emerge from analyses of these data, we decided to sample each family with sequences from at least two more representative genera. Thus, the families Apiaceae, Asteraceae, Brassicaceae, Caprifoliaceae, Chenopodiaceae, Fabaceae, Malvaceae, Poaceae, Polygonaceae, Ranunculaceae, and Solanaceae have each been sampled at least three times. These early results were published in a series of papers (Martin et al., 1983; Martin & Dowd, 1984a, b, c).

The sequences for rubisco-SSU, cytochrome c, and plastocyanin were analyzed for these families by Martin, Boulter, and Penny (1985) using derived estimates of familial node sequences. Analyses of data from single macromolecules were not consistent with one another but, for nine of the families, a phylogenetic tree derived from combined data remained consistent when ferrodoxin or 5S-ribosomal RNA (available for some of the families) was added.

This result indicated the need for longer sequences and better sampling of families. Although rubisco-SSU was always multiply represented, in 17 of the 33 samples of other macromolecules there was only a single sequence. This situation is precarious because, if the average distance from a familial node to a species is N, then on the average a single sequence will misrepresent the familial node by N. This source of error might be responsible for part of the poor agreement observed. Sampling a family at least twice, preferably from widely divergent representatives should give a better estimate of the familial node (see phase 5).

In phase 2 we sequenced rubisco-SSU from 11 members of Onagraceae (Martin & Dowd, 1986a), 15 monocotyledons (Martin & Dowd, 1986b), and 14 species of *Solanum* (Martin et al., 1986). We reasoned that the reliability of our methods might be estimated by comparison with taxonomically well understood groups. The results were similar to other taxonomic treatments. Additional species of Asteraceae were also studied and those results will be presented in this paper.

To estimate the rate of evolution, Proteaceae, Solanaceae, Fagaceae, and Winteraceae were sampled in phase 3 using species whose ancestors are thought to have been separated by continental drift at known times. This led to a preliminary publication (Martin & Dowd, 1984b), and the derivation of a molecular evolutionary clock (Martin & Dowd, 1988), which indicated that on average one nucleotide difference arose between two diverging lines once in seven million years.

In phase 4 we tested the hypothesis that leghemoglobin had evolved in plants by lateral transfer from animals. This led to an investigation of all species for which leghemoglobin sequences had been published, and it was shown that the pathway of evolution in those species was closely parallel in hemoglobin and rubisco-SSU (Martin & Dowd, 1986c), suggesting that there was no need to invoke novel evolutionary processes. A consequence of this study was that we increased the number of species of Fabaceae sequenced to eight (see Group 14 below) and obtained sequences from several additional families. Many of these were too small to be studied in the normal course of this investigation but were obtained either because they are known to include nitrogen-fixers or thought to be relatives of the legumes; these include Betulaceae, Casuarinaceae, Chrysobalanaceae, Coriariaceae, Crossosomataceae, Datiscaceae, Elaeagnaceae, Moringaceae, and Myricaceae.

In phase 5 we surveyed the dicotyledons which increased the number of families studied from 24 to 124.

A Survey of the Dicotyledons

There are about 250 families of dicots. Because it was impractical to sample all of them, a decision was made to sample about half, i.e., to increase the number from the 24 mentioned above to 124. Three families (Acanthaceae, Loranthaceae, Santalaceae) failed for reasons that will be discussed later. The additional 97 families were chosen primarily on the basis of size. The majority of families sampled have more than 20 genera. To cover as wide a range of variation as possible, some small families were also sampled. For example, the order Illiciales has only three genera, so the family Schisandraceae (two genera) was chosen to represent it. Only three orders are unrepresented out of Thorne's 41 (two of which are parasitic and devoid of rubisco), 10 out of Cronquist's 58, 19 out of Takhtajan's 72, and 21 out of Dahlgren's 85.

It is impractical, mainly because computers are limited in their capacities to analyze large numbers of taxa simultaneously, to contemplate building a phylogenetic tree for 122 families (comprising 310 species) without some subdivision into groups. We have done this by referring to all four current phylogenies. Thorne (1983) and Dahlgren (1983) have superorders as their major groups, the former nominating 19 and the latter 25. If these two authors agree that families are in the same superorder then they have been grouped together in our scheme, with one proviso. Takhtajan (1983) and Cronquist (1981) have respectively seven and six subclasses as their major groups, and these two authors have been allowed a veto; if either if them does not also agree that families are in the same subfamily, then they are left ungrouped. In this way we have divided 102 of the studied families into 25 Groups, leaving 20 ungrouped because there is disagreement. We are reluctant to use a formal term like superorder but need to make it clear that our use of Group does have a defined meaning, so we have used a capital G. The Groups are shown in Table 1.

It was practicable to sample each new family only twice, and we have done this by choosing two species not only from different genera but, if possible, from different subfamilies or tribes. Sometimes this criterion has broken down because fresh leaves have not been available.

In Table 2 the 335 species for which sequences are available are arranged by families and Groups, and their sources and sequences are given.

Biochemical Methods

The methods published by Martin and Jennings (1983) have stood the test of time, so, rather than repeat them here, a general description will be given and the few modifications mentioned.

Two methods were described, one for "pungent" leaves with high concentrations of phenolics or other substances that make protein purification difficult, the other for "bland" species whose leaves are much more amenable. The bland method gives better quality protein and is therefore to be preferred. However, because the pungent method works well with bland leaves, but not vice versa, it was preferred when there was doubt or too few leaves for trial extractions.

Both procedures started with maceration of about 100 g of leaves from which the midribs were removed if practicable. For bland leaves the extracting buffer was essentially a reducing, saline tris-HCl buffer at pH 7.4, while for pungent leaves a reducing, saline borate buffer at pH 8.6 and containing the detergent Triton X-100 was used. After crude straining and centrifugation to remove solids, the extract was passed through a succession of two liquid gel columns. A Sephadex G-25 column was used first to remove low molecular weight substances. A Sepharose 6B column was used to remove remaining low molecular weight substances and high molecular weight nucleic acids and membrane fragments. Eluting buffers were different for the two extraction procedures and for the different columns used. The protein was precipitated with ammonium sulfate for the bland method and with acetone for pungent. Procedures after the second column were the same for both types of leaves. The protein was S-carboxymethylated at pH 8.6 to break disulphide bridges between cysteine residues and then passed through a long column of Sephadex G-100 in an eluting buffer containing sodium dodecyl sulfate. This separated the large subunit from the small subunit, which was precipitated in acetone and dried before sequencing. (A variation of this procedure was to use a column of G75 followed by G-100.)

The methods are rather crude but are successful because rubisco is a very large protein and, by a considerable margin, the most abundant protein in leaves.

About 5 mg of small subunit (in 0.5 ml of water without polybrene) was sequenced on the Beckman

TABLE 1. Families of dicotyledons grouped because they are placed in the same major taxon by all of Cronquist (1981), Dahlgren (1983), Takhtajan (1983), and Thorne (1983).

GROUP 1	GROUP 4	GROUP 9	GROUP 12	GROUP 17	GROUP 21
Magnoli	Ulm	Dipterocarp	Eric	Connar	Lami
Winter	Mor	Elaeocarp	Epacrid	Sapind	Verben
Annon	Urtic	Tili	GROUP 13	Anacardi	GROUP 22
Myristic	GROUP 5	Sterculi	Cunoni	Simaroub	Solan
Schisandr	Hamamelid	Bombac	Ros	Meli	Convolvul
Monimi	Betul	Malv	Saxifrag	Rut	Polemoni
Laur	Fag	GROUP 10	GROUP 14	GROUP 18	GROUP 23
Aristoloch	Casuarin	Viol	Caesalpini	Halorag	Scrophulari
Calycanth	GROUP 6	Flacourti	Mimos	Rhizophor	Gesneri
GROUP 2	Dilleni	Datisc	Papilioni	GROUP 19	Bignoni
Berberid	Thea	Cucurbit	GROUP 15	Zygophyll	Pedali
Ranuncul	Ochn	Salic	Trap	Gerani	GROUP 24
Lardizabal	Clusi	Cappar	Lyth	Tropaeoli	Valerian
Menisperm	GROUP 7	Brassic	Myrt	Malpighi	Caprifol
Papaver	Myric	Resed	Punic	GROUP 20	GROUP 25
GROUP 3	Jugland	Moring	Onagr	Logani	Api
Cabomb	GROUP 8	GROUP 11	Melastomat	Gentian	Arali
Nymphae	Caryophyll	Sapot	Combret	Apocyn	
	Nyctagin	Styrac	GROUP 16	Asclepiad	
	Amaranth	Primul	Olac	Ole	
	Phytolacc	Myrsin	Celastr	Rubi	
	Chenopodi				

FAMILIES THAT DO NOT FIT INTO ONE OF THE GROUPS

Aster	Coriari	Goodeni	Nelumbon	Polygon	Thymelae
Bux	Crossosomat	Hydrophyll	Piper	Prote	Vit
Campanul	Elaeagn	Lecythid	Plumbagin	Rhamn	
Chrysobalan	Euphorbi	Loas			

Note: "-aceae" omitted from all names.

890C automatic sequencer using Beckman's standard quadrol program with 50% quadrol buffer. The phenylthiohydantoin (PTH) derivatives of the amino acids were identified using a Waters HPLC instrument with a C-18 radially compressed column and eluted with 0.1M sodium acetate (pH 6.0) and acetonitrile. This did not distinguish two pairs of amino acids and was therefore supplemented with TLC.

Using these methods, we could, without assistance, produce two proteins each week and sequence two others.

FAILURES

Although 90% of attempts led to successful sequences, the remaining 10% deserve brief attention. Unless there was an identified reason for failure that could be corrected, our policy was to try another representative of the family.

Faults that could be corrected include the amounts of extraction and elution buffers used. Some plants gave extracts that were mucilaginous to the point of setting solid. Dilution of the extract corrected this. This problem occurred in Onagraceae and a few others with small leaves containing a high proportion of veins. Insolubility of the protein, leading to precipitation in columns, could sometimes be corrected by loading a more dilute extract. Plants with C4 photosynthesis, and rubisco tightly bound in bundle sheaths, were avoided if possible. Plants with C3 photosynthesis often occur in the same genera or families and were unlikely to be phylogenetically biased. However, if unavoidable (e.g., *Welwitschia* is reported to be C4), special care was taken during the maceration process.

It is suspected that the most common cause of failure was the presence of powerful proteases in the leaves and, in retrospect, it would have been profitable to try correcting this with research early in the project. Species of *Ficus*, known to have leaf proteases, showed symptoms of this failure. Large amounts of protein traveled where the small subunit should have been on the G-100 column and gave many amino acids at each position when sequenced. Another casualty of this sort was *Gnetum gnemon*, which was particularly desired because it is a gymnosperm thought to be close to

TABLE 2. Species studied and sequences.

Notes:
(1) The dicotyledons are arranged by Groups as explained in the text and Table 1. After each family name we give the three-letter abbreviation of Weber(1982).
(2) After the species name and author, a slash is followed by the source of the specimen: P.G.=Private Garden (in Adelaide unless otherwise stated); B.G.=Botanic(al) Garden(s). Australian states: N.S.W.=New South Wales; N.T.=Northern Territory; Qld=Queensland; S.A.=South Australia; Vic.=Victoria; W.A.=Western Australia. N.Z.=New Zealand. C.S.I.R.O.=Commonwealth Scientific and Industrial Research Organisation. C.S.=certified seed.
(3) Key to N-terminal 40 amino acids:
A, alanine; D, aspartic acid; E, glutamic acid; F, phenylalanine; G, glycine; I, isoleucine; K, lysine; L, leucine; M, methionine; N, asparagine; P, proline; Q, glutamine; R, arginine; S, serine; T, threonine; V, valine; W, tryptophan; Y, tyrosine.

D I C O T Y L E D O N S.	
GROUP 1	
ANNONACEAE ANN	
Desmos goezeanus (F.Muell.)Jessop/N.Qld	M M V W P P E G K K K F E T L S Y L P S L S S E Q L A K E V E Y L L L N G W I P
Xylopia maccraei (F.Muell.)L.S.Smith/N.Qld	M M V W P P E G K K K F E T L S Y L P T L S S E E L A K E V E Y L I I S G W I P
ARISTOLOCHIACEAE ARS	
Aristolochia baetica L./Adelaide B.G.	M Q V W P P E G L K K F E T L S Y L P T L T E E Q L A K E I E Y L L L K G W V P
Asarum canadense L./Missouri B.G.	M Q V W P P E G L K K F E T L S Y L P P L S S Q E L A K E V D Y L L I K G W I P
CALYCANTHACEAE CAL	
Calycanthus floridus L./Adelaide B.G.	M Q V W P P E G L K K F E T L S Y L P P L S T E Q L I K E V D Y L L L K G W V P
Chimonanthus praecox (L.)Link./Adelaide B.G.	M Q V W P P E G L K K Y E T L S Y L P P L S S E Q L I K E I D Y L L L V G W V P
Idiospermum australiense (Diels)S.T.Blake/N.Qld	M Q V W P PV/EG L P K F E T L S Y L P P L V T E QI/LA K E I D Y L L L N G W V P
LAURACEAE LAU	
Laurus nobilis L./Adelaide B.G.	M L V W PP/TV/EGL K K F E T L S Y L P P L S S Q Q L A K E V D Y L L I S G W V P
Persea americana Mill./P.G.	M M V W P PV/EG L K K F E T L S Y L P P L S P E Q L A A E V D Y L L L S G W V P
MAGNOLIACEAE MAG	
Liriodendron tulipiferum L./P.G.	M L V W P P V G L K K F E T L S Y L P P L S P Q S L A K E V D Y L L R S G W I P
Magnolia soulangiana Soul.-Bod./P.G.	M L V W P P E G L K K F E T L S Y L P P L S S E E L A K E I D Y L I G S G W I P
Michelia figo (Lour.)Sprengl/Adelaide B.G.	M L V W P P E G L K K F E T L S Y L P P L S S E E L A K E I D Y L I R S G W I P
MONIMIACEAE MNM	
Peumus boldus Molina/Adelaide B.G.	M M V W P P E G L K K F E T L S Y L P P L S S E A L A K E V D Y L L I M G W V P
MYRISTICACEAE MYS	
Knema latericia Elmer/Singapore B.G	M M V W P P L G N K K F E T L S Y L P P V SV/ME Q L A K E I D Y L L L N G W V P
Myristica fragrans Houtt./Singapore B.G.	M M V W P P L G S K K F E T L S Y L P P L S L E Q L A K E I D Y L L L N G W V P
SCHISANDRACEAE SCS	
Kadsura japonica Dunal/Berkeley B.G.	M K V W P P Y N M K K F E T L S Y L S P I S Q E E L I K E I E Y L L L K G W V P
Schisandra rubriflora Rehder & Wilson/Kew B.G.	M Q V W P P Y N M K K F E T L S Y L S P L S Q E E L L K E I E Y L L L N G W V P
WINTERACEAE WIN	
Drimys winteri Forster/Kew B.G.	M K V W P P K G L L K F E T L S Y L P P L S S E Q L A K Q V E Y L I K M G W V P
Pseudowintera colorata (Raoul)Dandy/North N.Z.	M K V W P P K G L L K F E T L S Y L P P L S P Q Q L A K Q I D Y L I Q S G W V P
Tasmannia purpurascens (J.W.Vickery)A.C.Smith/ Canberra B.G.	M K V W P P K G L L K F E T L S Y L P P L S P G Q L A K Q V D Y L I K S G W V P
GROUP 2	
BERBERIDACEAE BER	
Berberis aetnensis Presl/Adelaide B.G.	M Q V W P P V G L K K F E T L S Y L P P L S S Q S L A K E V D Y L L L V G W V P
Nandina domestica Thunb./P.G.	M Q V W P P I G L K K F E T L S Y L P P L S P E A L A K E V D Y L L L K G W V P

TABLE 2. Continued.

LARDIZABALACEAE LAR	
Akebia quinata (Houtt.)Decne./Adelaide B.G.	M Q V W P P I G L K K F E T L S Y L P P L T Q E Q L A K E V E Y L L S S G W V P
Decaisnea fargesii Franchet/Kew B.G.	M Q V W P P V N L K K F E T L S Y L P P L S Q E Q L L K E V D Y L I N N G W I P
Lardizabala biternata Ruiz & Pav./Edinburgh B.G.	M K V W P P V G L K K F E T L S Y L P P L S Q E A L A K E I D Y L L S N G W V P
MENISPERMACEAE MNS	
Cocculus trilobus (Thunb.)DC./Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L S P Q A L A K E V D Y L L L N G W I P
Hypserpa laurina (F.Muell)Diels/Canberra B.G.	M K V W PP/VL G L K K F E T L S Y L P P L S P Q A L A K E V D Y L L L K G W I P
PAPAVERACEAE PAP	
Eschscholtzia californica Cham./Adelaide B.G.	M Q V W P P T G L K K F E T L S Y L P P L T A E Q L A K E V D Y L L K N G W V P
Papaver orientale L./P.G.	M Q V W P P T G L K K F E T L S Y L P D L T V E Q L A K E I D Y L L R N G W V P
Dicentra spectabilis Lem./P.G.	M Q V W E P Y N N K K F E T L S Y L PD/PL T V E Q L A K E V D Y L L L K G W V P
Fumaria officinalis L./P.G.	M K V W P P Y G M K K F E T L S Y L P Q L S Q E E L A K E V D Y L I S N G W V P
RANUNCULACEAE RAN	
Aquilegia vulgaris L./P.G.	M K V W P P L G L L K F E T L S Y L P P L S Q Q A L A K E V D Y L L A N G W V P
Clematis rehderiana Craib/Adelaide B.G.	M K V W Q P Y N N K K F E T L S Y L P E L T P E S L A K E IE/DY L I R K G W V P
Clematis viticella L./Adelaide B.G.	M K V W Q P Y N N K K F E T L S Y L P E L T E S Q I L K E I D Y L I R K G W V P
Helleborus foetidus L./Adelaide B.G.	M K V W P P L N N L K F E T L S Y L P P L S Q A S L A K E V D Y L I V K G W I P
Ranunculus trilobus Desf./P.G.	M K V W N P V G N Q K F E T L S Y L P P L S T E S L A K E V E Y L I R K G W V P
GROUP 3	
CABOMBACEAE CAB	
Brasenia schreberi Gmelin/Nagambie Vic.	M A V W P I YN/VL K K F E T L S Y L P S L S K E Q L A K E V E Y L L I K K W I P
NYMPHAEACEAE NYM	
Nuphar advena W.T.Aiton/Canberra Public garden	M K V W P P YN/DVQ/KK Y E T L S Y L P P L S T E Q L A K E V D Y L L S N K W I P
Nymphaea gigantea Hook./P.G.	M K V W N P Y N N I K F E T L S Y L P P L T D E Q L A K E V E Y L L L S K W I P
Victoria amazonica (Poeppig)Sowerby/Adelaide B.G.	M K V W P P Y N N I K F E T L S Y L P P L S D E Q L A K E V E Y L L L K K W I P
GROUP 4	
MORACEAE MOR	
Humulus scandens (Lour.)Merr./Adelaide B.G.	M K V W P P S N V K K F E T L S Y L P P L S V E Q L L K E V E Y L L K S G W V P
Morus alba L./Adelaide B.G.	M K V W P P S G L L K F E T L S Y L P D L T S E Q L I K E I D Y L L L S N W I P
ULMACEAE ULM	
Parasponia andersoni Planch./CSIRO Canberra	M Q V W P P L G K K K F E T L S Y L P E L T I E Q L I K Q I E F L I K K G W V P
Ulmus parvifolia Jacq./Adelaide B.G.	M Q V W P P P G Y K K F E T L S Y L P D L T T E Q L I K E V E Y L L L K G W V P
URTICACEAE URT	
Parietaria judaica L./Adelaide B.G.	M Q V W P P S G L K K F E T L S Y L P D L T E E Q L I K E V D Y L I K SKL/WI/VP
Pipturus argenteus Wedd./Adelaide B.G.	M Q V W P P S G L K K F E T L S Y L P P L T E A Q L L K Q I D F L I K S K L I P
GROUP 5	
BETULACEAE BET	
Alnus maximowiczii Callier/Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L T A E Q L A K E V D Y L L L K G W I P
Betula atrata Domin./Adelaide B.G.	M Q V W P P L G L K K F E T L S Y L P P L T T E Q L A K Q V D Y L L K N G W I P
CASUARINACEAE CAS	
Allocasuarina muelleriana (Miq.)L.Johnson/ Adelaide B.G.	M Q V W P P L G K K K F E T L S Y L P P L S S E S L A K E V D Y L L L K K W I P
Casuarina glauca Sieber/Adelaide B.G.	M Q V W P P L G K K K F E T L S Y L P N L S S E S L A K E V D Y L L L K K W I P
Gymnostoma (sp. nov. L.Johnson)/N.Qld	M Q V W P P S G K K F F E T L S Y L P Q L S S E S L A K E V D Y L L L K K W I P
FAGACEAE FAG	
Fagus sylvaticus L./P.G.	M K V W P P L G L Q K F E T L S Y L P P L V S E N L A K Q I E Y L L N K G W I P
Nothofagus aequilateralis (Baum.-Bodenh.)Steenis/	M K V W P P L G L I K F E T L S Y L P P L S S E I L A K E V D Y L I S S G W I P

TABLE 2. Continued.

	New Caledonia
Nothofagus antarctica (Forster)Oersted/Kew B.G.	M K V W P P L G L K K F E T L S Y L P T L T P A E L A K E V D Y L L R K G W V P
Nothofagus betuloides (Mirbel)Oersted/Kew B.G.	M K V W P P L G L K K F E T L S Y L P P L T P E N L A K E V D Y L L N K G W V P
Nothofagus cunninghamii Ostenfeld/Cape Otway Vic.	M K V W P P L G L K K F E T L S Y L P P L T N E N L A K E V D Y L L R K G W V P
Nothofagus fusca (Hook.f.)Oersted/Otari B.G. N.Z.	M K V W P P L G L K K F E T L S Y L P P L S S E A L A K E V D Y L I S K G W V P
Nothofagus gunnii Hook.f./Tasmania	M K V W P P L G L K K F E T L S Y L P P L S P E Q L A L K V D Y L L R K G W V P
Nothofagus menziesii (Hook.f.)Oersted/ Wellington B.G. N.Z.	M K V W P P L G L K K F E T L S Y L P P L S S E S L A K E V D Y L L R K S W V P
Nothofagus moorei F.Muell/New England NSW	M K V W P P L G L K K F E T L S Y L P P L T P E S L A K E V D Y L L R K G W V P
Nothofagus procera (Poeppig & Endler)Oersted/ Kew B.G.	M K V W P P L G L K K F E T L S Y L P P L T P A E L A K E V D Y L L R K G W V P
Nothofagus pumilio (Poeppig & Endler)Krasser/ Kew B.G.	M K V W P P L G L K K F E T L S Y L P P L S P E S L A K E V D Y L L L K G W V P
Nothofagus solandri (Hook.f)Oersted/Otari B.G. N.Z.	M K V W P P L G L K K F E T L S Y L P P L S L E A L A K E V D Y L I S K G W V P
Quercus robur L./P.G.	M Q V W P P L G K K K Y E T L S Y L P P L T D E Q L G R E I D Y L L R S G W V P
HAMAMELIDACEAE HAM	
Liquidambar styraciflua L./Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L S N A A L A K E V D Y L L R S G W V P
Parrotia persica C.Meyer/Adelaide B.G.	M K V W P T E N N L K F E T L S Y L P P L T N A D L A K E V D Y L L R S G W I P
GROUP 6	
CLUSIACEAE CLU	
Garcinia mangostana L./CSIRO Darwin N.T.	M Q V W P P L G L K K F E T L S Y L S P L S L A E L A K E V D Y L L L S K W I P
Hypericum hookerianum Wight & Arn./Adelaide B.G.	M Q V W P P L G L K K F E T L S Y L P P L S I E Q L A K E V D Y L I I S G W I P
DILLENIACEAE DLL	
Dillenia alata (DC.)Martelli/Canberra B.G.	M K V W P P S G L L K F E T L S Y L P D L S S Q E L A K E V D Y L L R M G W I P
Hibbertia scandens (Willd.)Gilg/P.G.	M L V W P P E G L K K F E T L S Y L P P L S P Q E L LK/LE V A Y L L L K G L I P
OCHNACEAE OCH	
Brackenridgea nitida A.Gray/N.Qld	MK/QV W P T E G L S K F E T L S Y L P D L T E A Q L I K E I D Y L I I K G W I P
Ochna atropurpurea DC./Adelaide B.G.	M K V W P T E G L K K F E T L S Y L P S L T Q A Q L I K E V D Y L L I K G W I P
THEACEAE TEA	
Gordonia axillaris Szyszyl./Mt Lofty B.G. S.A.	M K V W S P L G L K K F E T L S Y L P S L T N I Q L A K E V D Y L I N K G W I P
Ternstroemia cherryi (F.M.Bailey)Merr. ex J.F.Bailey& C.T.White/N.Qld	M M V W P P L G L K K F E T L S Y L P S L S D I E L A K E V D Y L L L S G W V P
GROUP 7	
JUGLANDACEAE JUG	
Carya illinoensis (Wangenh.)Koch/Adelaide B.G.	M Q V W P P L G K K K F E T L S Y L P P L S P A Q L A K E V D Y L L S K G W I P
Juglans regia L./Adelaide B.G.	M Q V W P P L G K K K F E T L S Y L P P L T A E S L A K E V D Y L I S K G W I P
MYRICACEAE MYR	
Myrica pennsylvannica Loisel/Adelaide B.G.	M Q V W P P L G K K K F E T L S Y L P P L S P A A L A K E V D Y L L R K G W I P
GROUP 8	
AMARANTHACEAE AMA	
Bosea amherstiana (Moq.)Hook./Adelaide B.G.	M Q V W P P L GK/LK K F E T L S Y L P P L S Q E S L T K E V S Y L L L K G W V P
Celosia argentea L./P.G.	M Q V W P PT/LG K K K F E T L S Y L S P L S Q E Q L L K Q V S Y L L N K G W V P
CARYOPHYLLACEAE CRY	
Cerastium tomentosum L./Adelaide B.G.	M Q V W P P T G L K K F E T L S Y L P P L S E E Q L L K E I N Y L L I K G W V P
Silene colorata Poiret/Adelaide B.G.	M Q V W P P S N L K K F E T L S Y L P P L T E E Q L L K E I N Y L L V K G W V P
CHENOPODIACEAE CHN	
Beta vulgaris L./C.S.	M Q V W P P L G L K K F E T L S Y L P P L T T E Q L L A E V N Y L L V K G W I P
Chenopodium murale L./P.G.	M Q V W P P V G K K K F E T L S Y L P P L S P E S L L G E V E Y L L N K G W V P

TABLE 2. Continued.

Spinacia oleracea L./C.S.	M Q V W P P L G L K K F E T L S Y L P P L T T E Q L L A E V N Y L L V K G W I P
NYCTAGINACEAE NYC	
Bougainvillea glabra Choisy/Adelaide B.G.	M Q V W P P T G K I K F E T L S Y L P P L T P E Q L L K E V Q Y L L N K G W V P
Mirabilis jalapa L./Adelaide B.G.	M Q V W P PI/LG K K I F E T L S Y L P T L T S E Q L L K E V Q Y L L N K G W V P
PHYTOLACCACEAE PHT	
Codonocarpus cotinifolius (Desf.)F.Muell./North S.A	M Q V W P T V G L K K F E T L S Y L P D L N E E S L A K E V D Y L L L K G W I P
Phytolacca dioica L./Adelaide B.G.	M Q V W P TV/LGL/KK K F E T L S Y L P P L S Q E S L T K E V E Y L L N K G W V P
GROUP 9	
BOMBACACEAE BOM	
Chorisia insignis Kunth/Adelaide B.G.	M Q V W P P L G K K K F E T F S Y L P D L V T E E L I K E I E Y L I L K K W I P
Durio zibethinus L./CSIRO Darwin N.T.	M K V W P P L G I K K F E T F S Y L P D L S T D E L L K E I E Y L L L K K W I P
DIPTEROCARPACEAE DPC	
Dryobalanops aromatica Gaertner/Singapore B.G.	M Q V W P P L G K K K F E T L S Y L P D L T P E Q L A K E V D Y L L L S K W I P
Shorea pauciflora King/Singapore B.G.	M Q V W P P L G K K K F E T L S Y L P D L S P E Q L A K E V D Y L L L S K W V P
ELAEOCARPACEAE ELC	
Aristotelia australasica F.Muell./Canberra B.G.	M Q V W P P L G K K K F E T L S Y L P P L S A A E L A K E V D Y L L L K G W V P
Eleocarpus grandis F. Muell./Adelaide B.G.	M Q V W P P I G L K K F E T L S Y L P P L S T A A L A K E I D Y L L L K G W V P
MALVACEAE MLV	
Althaea rosea (L.)Cav./P.G.	M K V W P P L G L K K F E T L S Y L P P L T T E Q L A K E V E Y L L R K K W V P
Malva parviflora L./P.G.	M K V W P P L G L K K F E T L S Y L P P L T S E Q L A K E V E Y L L R K K W V P
Sphaeralcea umbellata (Cav.)G.Don/Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P T L T D E Q L A K E V E Y L L R S K W V P
STERCULIACEAE STR	
Brachychiton discolor F.Muell./Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L S T E E L L K E V E Y L I L S N W I P
Dombeya mastersi Hook f./Adelaide B.G.	M K V W P P E G L K K F E T L S Y L P D L S T E Q L L K E I D Y L I I S N W I P
TILIACEAE TIL	
Grewia occidentalis L./Adelaide B.G.	M K V W P P I N K K I F E T L S Y L P P L T V T Q L A K E V D Y L L L N G W I P
Sparmannia africana L.f./Adelaide B.G.	M K V W P T E G L K K F E T L S Y L P T L T D E Q L L K E I D Y L I R K K W I P
GROUP 10	
BRASSICACEAE BRA	
Brassica napus L./C.S.	M K V W P P VG/AK K K F E T L S Y L P D L T E V E L G K E V D Y L L E N K W I P
Nasturtium officinale R.Br./P.G.	M Q V W P P I G K K K F E T L S Y L P D L T D V E L G K E V D Y L L R N K W I P
Raphanus sativus L./C.S.	M K V W P P I G K K K F E T L S Y L P D L T D V E L G K E V D Y L L R N K W I P
CAPPARACEAE CPP	
Cleome spinosa L./P.G.	M Q V W P T T G L R K F E T L S Y L P D L S D D E L A K E V D Y L L L N N W I P
CUCURBITACEAE CUC	
Cucumis sativus L./P.G.	M K V W P P L G L R K F E T L S Y L P D M S N E Q L S K E R D Y L L S N G W V P
Cucurbita pepo L./P.G.	M K V W P P L G L K K F E T L S Y L P D L S D A Q L L K E I G Y L L L S G W V P
DATISCACEAE DAT	
Datisca cannabina L./Adelaide B.G.	M K V W P P L G.L K K Y E T L S Y L PP/DL T T E Q L S K E V E Y L I I V G W I P
Tetrameles nudiflora R.Br./N.Qld	M Q V W P P V G K K K F E T L S Y L P P L T D E Q L S K E V E Y L L I S K W I P
FLACOURTIACEAE FLC	
Azara celastrina D.Don/Adelaide B.G.	M Q V W P P V G L K K F E T L S Y L P D L T S E Q L A K E I E Y L L I S K W V P
Kiggelaria africana L./Adelaide B.G.	M Q V W P P L G K K K F E T L S Y L P D L T S E E L A K E V E Y I L L N K W I P
MORINGACEAE MRG	
Moringa oleifera Lam./Lyon Arboretum Hawaii	M Q V W P P T G L K K F E T L S Y L P P L S A E E L A K E V D Y L L L K G W I P
RESEDACEAE RSD	
Reseda luteola L./Adelaide B.G.	M Q V W P P L G L K K F E T L S Y L P D L S D E E L A K E V D Y L L S N K W I P
SALICACEAE SAL	

TABLE 2. Continued.

Populus nigra L./Adelaide B.G.	M Q V W P P L G L K K F E T L S Y L P D L S T E Q L A K E I Q Y L L L N K W V P
Salix babylonica L./Adelaide B.G.	M Q V W P V L G L K K F E T L S Y L P D L T K E Q L A K E I E Y L L L S K W V P
VIOLACEAE VIO	
Melicytus ramiflorus Forster/Adelaide B.G.	MK/QV W P T V G L K K F E T L S Y L P P L T S E Q L A K E I D Y L I I K G W I P
Viola odorata L./P.G.	M K V W P T T G L K K F E T L S Y L P P L T T E Q L A K E I D Y L I S N G W I P
GROUP 11	
MYRSINACEAE MRS	
Ardisia humilis Vahl/Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L T E A Q L A K E I E Y L L L S G W V P
Rapanea variabilis (R.Br.)Mez/Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L T I E Q L A K E I D Y L L L S G W I P
PRIMULACEAE PRM	
Cyclamen neapolitanum Ten./P.G.	M K V W P P L G L K K F E T L S Y L P P L S S E Q L L K E V D Y L L L N G W V P
Primula malacoides Franchet/P.G.	M K V W P P L G L K K F E T L S Y L P P L T V E Q L L K E V D Y I I I N G W I P
SAPOTACEAE SPT	
Mimusops cyanocarpa Cunn. ex Sweet/Adelaide B.G.	M T V W P P L G L K V F E T L S Y L P P L T Y E E L A A E V D Y L I I S K W I P
Planchonella australis (F.Muell.)Pierre/ Adelaide B.G.	M S V W P P K G L K L F E T L S Y L P P L S Y E E L A A E V D Y I L L S K W I P
STYRACACEAE STY	
Halesia carolina Ellis/Missouri B.G.	M K V W P P L G L K K F E T L S Y L P P L S D N E L L K E I N Y L I L S G W I P
Styrax japonica Sieber & Zucc./Missouri B.G.	M M V W P T E G L K K F E T L S Y L P P L T D E E L L K E I E YI/LL L S G W I P
GROUP 12	
EPACRIDACEAE EPC	
Astroloma conostephioides (Sonder)F.Muell./ Montacute S.A.	M K V W P P I G IIK K F E T L S Y L P P L T D E Q L L K E V D Y L I N K G W I P
Leucopogon parviflorus Lindley/Sellick's Beach S.A.	M K V W P P I G IIK K F E T L S Y L P P L T D Q Q L L K E V D Y L I I K G W V P
ERICACEAE ERI	
Arbutus andrachne L./Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L S I P S L A K E I E Y L I I Q G W I P
Rhododendron ponticum L./Mt Lofty B.G. S.A.	M K V W P P I G L V K F E T L S Y L P P L S T E Q L L K E V D Y L I I K G W V P
GROUP 13	
CUNONIACEAE CUN	
Aphanopetalum resinosum Endl./Canberra B.G.	M K V W P P V G L K Y F E T L S Y L P P L S Q A Q L A K E V D Y L L L K G W V P
Callicoma serratifolia Andr./Canberra B.G.	M K V W P P L G L K K F E T L S Y L P P L T T A E L A K E V D Y L L L S G W I P
ROSACEAE ROS	
Prunus ilicifolia Walp./Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L S P E E L A K E V D Y L L L K N W V P
Pyrus communis L./Adelaide B.G.	M Q V W P P L G L K K F E T L S Y L P P L S T E E L A K E V D Y L L L K N W V P
SAXIFRAGACEAE SAX	
Bergenia X schmidtii Silva-Tarouca/Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L T Q E E L A K E V E Y L L L S G W V P
Hydrangea paniculata Sieber/P.G.	M K V W P T A V L K K F E T L S Y L P P L T V E Q L G K E V D Y L L LK/RK W V P
GROUP 14	
CAESALPINIACEAE CSL	
Ceratonia siliqua L./Adelaide B.G.	M Q V W P P L G L K K F E T L S Y L P P L S S E E L G K E I D Y L L L K G W I P
Gleditsia triacanthos L./Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L S T E E L A K E V D Y L L R K G W I P
MIMOSACEAE MIM	
Acacia fimbriata Cunn. ex G.Don/Adelaide B.G.	M L V W P P L G K K K F E T L S Y L P P L T T E Q L A K Q V D Y L L L Q G W V P
Leucaena glauca Benth./Adelaide B.G.	M L V W P P L G K K K F E T L S Y L P T L T T E E L L A E V E Y L L R Q G W V P
PAPILIONACEAE PPL	
Glycine max Merr./P.G.	M Q V W P P I G K K K F E T L S Y L P D L D D A Q L A K E V E Y L L R K G W I P

TABLE 2. Continued.

Goodia lotifolia Salisb./Canberra B.G.	M Q V W P P L G K K K F E T L S Y L P P L T T E E L A K E V E Y L L L K G W I P
Hovea acutifolia A.Cunn./Canberra B.G.	M K V W P P I G L K K Y E T L S Y L P P L S S E E L L K E V E Y L L L K G W I P
Lupinus angustifolius L./C.S.	M K V W P PI/VG L K KF/YE T L S Y L P P L T T E S L A K E V D Y L I R N G W V P
Oxylobium lanceolatum (Vent.)Druce/Canberra B.G.	M Q V W P P I N K K K F E T L S Y L P P L S P E E L A K E V E Y L L L K G W I P
Pisum sativum L./C.S.	M Q V W P P I G K K K F E T L S Y L P P L T R D Q L L K E V E Y L L R K G W V P
Vicia faba L./C.S.	M Q V W P P I G K K K F E T L S Y L P P L TQ/RD Q L L K E V E Y L L R K G W V P
Vigna radiata (L.)Wilezek/C.S.	M Q V W P S I G K K K F E T L S Y L P D L T E E Q L G K E V D Y L L R K G W V P
GROUP 15	
COMBRETACEAE CMB	
Combretum decandrum Roxb./Adelaide B.G.	M K V W P P L G K K K F E T L S Y L S P L S Y E Q L L K E V D Y L L A N K W V P
Quisqualis indica L./Missouri B.G.	M K V W P P L G K K K F E T L S Y L S P L S S Q Q L L K E V D Y L L S N G W V P
LYTHRACEAE LYT	
Lythrum salicaria L./Adelaide B.G.	M Q V W P P E G L K K F E T L S Y L P P L T S E E L L K E V E Y L L L K G W V P
Woodfordia fructicosa (L.)Kurz/Adelaide B.G.	M Q V W P P L G K K K F E T L S Y L P P L T T T Q L A K E V D Y L L L K G W V P
MELASTOMATACEAE MLS	
Melastoma affine D.Don/North N.S.W.	M Q V W P P E N K K K F E T L S Y L P P L S S D Q L L K Q I A Y L I N K G W I P
Tibouchina urvilleana (DC.)Cogn./P.G.	M Q V W P P E N K K K F E T L S Y L P D L S S E Q L I K Q I A Y L I R S G W I P
MYRTACEAE MRT	
Acmena smithii (Poiret)Merr. & Perry/Adelaide B.G.	M Q V W P P T G K K K F E T L S Y L P T L S P E Q L A K E V D Y L I L S G W V P
Eucalyptus microcarpa (Maiden)Maiden/P.G.	M Q V W P P I G K K K F E T L S Y L P T L S S E Q L A K E V D Y L I K K G W V P
ONAGRACEAE ONA	
Circea cordata Royle/Missouri B.G.	F N V W P P E G L K K F E T L S Y L P T L T Q D Q L I K E V E Y L L R K G W V P
Clarkia rubicunda (Lindl.)Lewis & Lewis/P.G.	F N V W P P L G L K K F E T L S Y L P P L T T D Q L I K E V D Y L L K N N W V P
Clarkia unguiculata Lindl./P.G.	F N V W P P E G L K K F E T L S Y L P P L T A D Q L I K E V D Y L L K K G W V P
Epilobium canum (Greene)Raven/Adelaide B.G.	F N V W P P E G L K K F E T L S Y L P P L T R D Q L G K E V E Y L L R N G W V P
Epilobium ciliatum Raf./P.G.	F N V W P P E G L K K F E T L S Y L P P L T R E Q L I K E V E Y L L R N G W V P
Fuchsia hybrida Voss/P.G.	F N V W P P E G L K K F E T L S Y L P P L T Q E Q L I K E V E Y L L S N G W V P
Gaura lindheimeri Engelm. & A.Gray./Adelaide B.G.	F N V W P P E G L K K F E T L S Y L PP/DL TT/DE Q L I K E V E Y L I S N G W V P
Hauya elegans DC./Missouri B.G.	F N V W P P E G K K K F E T L S Y L P P L S T E Q L L K E V E Y L L R N G W V P
Lopezia semeiandra (Plitmann)Raven & Breedlove/Missouri B.G.	F N V W P P E G L L K F E T L S Y L P P L T Q E Q L L K E V D Y L LR/SK N W V P
Ludwigia peploides (Kunth)Raven/Milang S.A.	M K V W P P E G K K K F E T L S Y L P P L T D E Q L G K E V D Y L L S K G W V P
Oenotheria stricta Ledeb./Murray Bridge S.A.	F N V W P P E G L K K F E T L S Y L P P L S R E Q L I K E V E Y L I R N T W V P
PUNICACEAE PUN	
Punica granatum L./P.G.	M K V W P P L G L K K F E T L S Y L P P L S E A Q L G R E V D Y L L R S G W V P
TRAPACEAE TRA	
Trapa natans L.var.japonica Nakai/Japan	M Q V W P P E G L K K F E T L S Y L P P L T T E Q L L K E I E Y L I I S G W I P
GROUP 16	
CELASTRACEAE CEL	
Cassine papillosa (Hochst)Kuntze/Adelaide B.G.	M K V W P T I GL/YI K F E T L S Y L P P L S D E E L G A E V D Y L L S N G W I P
Euonymus japonica L./Adelaide B.G.	M K V W P T E G L I K F E T L S Y L P P L S D Q Q L A A E V D Y L L L S G W I P
OLACACEAE OLC	
Ochanostachys amentacea Masters/Singapore B.G.	M Q V W PT/PT GY/LK K F E T L S Y L P T L S P Q Q L A A E V N Y L L L N G W I P
Strombosia javanica Blume/Bogor B.G. Indonesia	M Q V W P S T G L K K F E T L S Y L P T L S A E Q L A A E V E Y L L L S G W I P
GROUP 17	
ANACARDIACEAE ANA	
Mangifera indica L./Brisbane P.G.	M L V W P P L G K K K F E T L S Y L S P L N S Q A L L K E II/FY L L L S G W V P

TABLE 2. Continued.

Pistacia atlantica Desf./Adelaide B.G.	M K V W P P V G L K K Y E T L S Y L S P LN/TS E E L L K E V Q Y L L L S K W I P
CONNARACEAE CNN	
Agelaea trinervis (Llanos)Merr./Bogor B.G.Indonesia	M K V W P P L G K K K F E T L S Y L L P L S T Q Q L A Q E V D Y L L L S G W V P
Connarus conchocarpus F.Muell./N.Qld	M K V W P P L G K K K F E T L S Y L P D M T P K Q L A K E V N Y L L L N G W V P
MELIACEAE MEL	
Cedrela sinensis A.L.Juss./Adelaide B.G.	M Q V W P PV/LG K K K F E T L S Y L P P L S T E E L G K E V D Y L L R S G S V P
RUTACEAE RUT	
Calodendrum capense Thunb./Adelaide B.G.	M K V W P T V G L K K F E T L S Y L P P L S P E E L L K E V D Y L L L M G W V P
Correa pulchella Mackay ex Sweet/P.G.	M K V W P T V G M K K F E T L S Y L P P L S P E Q L L K E V D Y L L L M G W V P
Flindersia collina Bailey/Adelaide B.G.	M Q V W P P F G K K K F E T L S Y L P P L S P E E L L K Q V D Y L L K K G W I P
SAPINDACEAE SAP	
Dodonaea viscosa Jacq./Ouyen Vic.	M K V W P T T G L K K F E T L S Y L P T L S S E E L A K E V N Y L L L K G W I P
Harpullia pendula Planchon ex F.Muell./Adelaide B.G.	M Q V W P P L G D K K F E T L S Y L P P L S L E Q L A K E I E Y L L L K G W I P
SIMAROUBACEAE SMR	
Ailanthus altissima (Miller)Swingle/Adelaide B.G.	M Q V W P P T G K K K F E T L S Y L P P L S P E E L L K E V D Y L L L K G S I P
Kirkia wilmsii Engl./Adelaide B.G.	M K V W P T L G L K K F E T L S Y L P P L S P E E L L K E I D Y L L L K G S I P
GROUP 18	
HALORAGACEAE HAL	
Gonocarpus oreophyllus A.E.Orchard/Canberra B.G.	M Q V W P P L G L K K F E T L S Y L P P L T T E Q L A K Q I D F L L L S K W V P
Haloragodendron bauerlenii (F.Muell.)A.E.Orchard/ Canberra B.G.	M K V W P P V G L K K F E T L S Y L P P L S P E E L A K Q V E F L L L Q G W V P
RHIZOPHORACEAE RHZ	
Anisophyllea disticha Baill./Kuching Forest Sarawak	M M V W P P I G K K Y F E T L S Y L P P L S S E A L A K E V E Y L I I K G W I P
Bruguiera exaristata Ding Hou/Darwin N.T.	M L V W P P E G K K K F E T L S Y L P P L T T E Q L S K E V D Y L L L S K W V P
Carallia brachiata (Lour.)Merr./Darwin N.T.	M Q V W P P I G K K K F E T L S Y L P P L S S E E L A K E V D Y L L L S K W I P
GROUP 19	
GERANIACEAE GER	
Erodium moschatum L'Her./P.G.	M K V W P P L G L K K F E T L S Y L P P L T Q E E L G K E V D Y L L L S G W V P
Pelargonium cucullatum (L.)Aiton/Adelaide B.G.	M E V W P P L G L K K F E T L S Y L P P L T P E E L G K E V D Y L L L S G W V P
MALPIGHIACEAE MLP	
Malpighia glabra L./Adelaide B.G.	M Q V W P T E G L S K F E T L S Y L P P L T D E E L I K E I D Y L L I S G W V P
Stigmaphyllon ciliatum (Lam.)Adr.Juss./Adelaide B.G.	M M V W P T L G L S K F E T L S Y L P P L S A E E L L K E V E Y L L L S G W I P
TROPAEOLACEAE TRP	
Tropaeolum majus L./Adelaide B.G.	M Q V W P P L G L K K F E T L S Y L P P L T E V Q L A K E I D Y L I R S G W I P
ZYGOPHYLLACEAE ZYG	
Zygophyllum apiculatum F.Muell./Balranald N.S.W.	M K V W P T L G L K K F E T L S Y L P T L S E E G L L K E I E Y L I I S G W I P
GROUP 20	
APOCYNACEAE APO	
Mandevilla laxa (Ruiz & Pavon)Woodson/Adelaide B.G.	M Q V W P F I N K K K Y E T L S Y L P D L T P Q Q L A K E V D Y L L L K G W I P
Vinca minor L./Adelaide B.G.	M K V W P F L G L K K F E T L S Y L P D L T E Q Q L A K E V D Y L L L K G W I P
ASCLEPIADACEAE ASC	
Hoya carnosa R.Br./P.G.	M Q V W P P V G K K K Y E T L S Y L P P L T N E Q L I K E I D Y L L L N K G I P
GENTIANACEAE GEN	
Eustoma russellianum G.Don/P.G.	M K V W P T E G L K K F E T L S Y L P P L T T E Q L A K E I D Y L L L S G W I P
Orphium frutescens E.Meyer/Adelaide B.G.	M K V W P P V N M K K F E T L S Y L P P L T T E Q L A K E V D Y L L L S G W V P
LOGANIACEAE LOG	
Buddleia globosa Hope/Mt Lofty B.G. S.A.	M K V W P P L G L K KF/YE T L S Y L P P L T D E Q L L K E I D Y L L L S K W I P

TABLE 2. Continued.

Logania vaginalis (Labill.)F.Muell./P.G.	M Q V W P T E G L K K F E T L S Y L P E L T E A Q L L K E V D Y L L L N G W I P
OLEACEAE OLE	
Fraxinus excelsior L./Adelaide B.G.	M K V W P P L G L K K Y E T L S Y L P D L S S E Q L L K E V D Y L L L S K W I P
Olea europaea L./Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P D L T S E Q L L K E V D Y L L L S K W I P
RUBIACEAE RUB	
Coprosma repens A.Rich./Adelaide B.G.	M K V W P P L G L K K Y E T L S Y L P P L T T E Q L I K E I E Y L I S M G W I P
Gardenia thunbergia L.f./Adelaide B.G.	M Q V W PP/TY G K K K Y E T L S Y L P P L T T E Q L I K E I D Y L I S T G W V P
GROUP 21	
LAMIACEAE LAM	
Phlomis cashmeriana Royle/Adelaide B.G.	M K V W P T E G L K K F E T L S Y L P P L T S E E L L K E V E Y L L L K N L I P
Teucrium flavum L./Adelaide B.G.	M K V W P P E GGGGV K F E T L S Y L P P L S S E Q L I K Q V E F L L L K N L I P
VERBENACEAE VRB	
Citharexylum myrianthum Cham./Adelaide B.G.	M K V W P T E G L K K F E T L S Y L P D L S T E Q L L K E V D F L L L K K L I P
Vitex lucens Kirk/Adelaide B.G.	M K V W P T E G L K K F E T L S Y L P P L T TE/KE L L K Q V E Y L L L S K L I P
GROUP 22	
CONVOLVULACEAE CNV	
Dichondra repens Forster & G.Forster/Adelaide B.G.	M Q V W P P V G L K K F E T L S Y L P P L S T E Q L L K Q V D Y L I R K G W V P
Ipomoea learii Paxton/P.G.	M Q V W P P IT/GL K K F E T L S Y L P D L S T E Q L L K Q V E Y L L N K G W V P
POLEMONIACEAE PLM	
Cobaea scandens Cav./P.G.	MQ/KV W P P L G L KK/EF E T L S Y L P E L T SQ/KE L A K E V D Y L L K K G W I P
Phlox paniculata L./P.G.	M K V W P P L G L K K F E T L S Y L P P L T D E Q L A K Q V D Y L L L E G W V P
SOLANACEAE SOL	
Anthocercis angustifolia F.Muell./Mt Lofty S.A.	M Q V W P P I N M K K Y E T L S Y L P D L S E E Q L L L E I E Y L L L S G W V P
Lycopersicum esculentum Millan/P.G.	M Q V W P P I N M K K Y E T L S Y L P D L T D E Q L L T E I E Y L L K N G W V P
Nicotiana africana Merxm./C.S.	M Q V W P P I N K K K Y E T L S Y L P D L S Q E Q L L L E I E Y L L K N S W V P
Nicotiana fragrans Hook./C.S.	M Q V W P P I N K K K Y E T L S Y L P D L S Q E Q L L L E I E Y L L K N G W V P
Nicotiana goodspeedii H.Wheeler/C.S.	M Q V W P P I N M K K Y E T L S Y L P D L S Q E Q L L L E V E Y L L K N G W V P
Nicotiana maritima H.Wheeler/C.S.	M Q V W P P I N M K K Y E T L S Y L P D L S Q E Q L L L E V E Y L L K N G W V P
Nicotiana petunioides (Grisebach)Millan/C.S.	M Q V W P P I N M K K Y E T L S Y L P D L S Q E Q L L L E I E Y L L K N G W V P
Nicotiana sylvestris Spegazzini & Comes/C.S.	M Q V W P P I N K K K Y E T L S Y L P D L S Q E Q L L L E V E Y L L K N G W V P
Nicotiana tabacum L./C.S.	M Q V W P PI/YN/GKK K Y E T L S Y L P D L S Q E Q L L L EV/IE Y L L K N G W V P
Petunia hybrida Vilm./P.G.	M Q V W P P Y G K K K Y E T L S Y L P D L T D E Q L L K E I E Y L L N K G W V P
Solanum aviculare G.Forster/P.G.	M Q V W P P I N K KT/KY E T L S Y L P D L T D E Q L L T E I E Y L L K N G W V P
Solanum chippendalei Symon/Alice Springs N.T.	M Q V W P P I G K K K Y E T F S Y L P D F S D E Q L L A E I D Y L L L S G W V P
Solanum cinereum R.Br./Wilpena S.A.	M Q V W P P IN/GK K K Y E T F S Y L P T F S D E Q L L A E I D Y L L R S G W V P
Solanum macrocarpon L./P.G.	M Q V W P P I N K K K Y E T L S Y L P D L S D E Q L L L E I D Y L L R S G W V P
Solanum marginatum L.f./P.G.	M Q V W P P I N K K K Y E T L S Y L P D L S S E Q L L L E I D Y L I R N G W I P
Solanum melongena L./P.G.	M Q V W P P I N K K K Y E T L S Y L P D L S D E Q L L L E I D Y L I L N G W V P
Solanum nigrum L./P.G.	M Q V W P P I N K K K Y E T L S Y L P D L S D E Q L L K E I D Y L L K N G W V P
Solanum oligacanthum F.Muell./P.G.	M Q V W P P IE/NK K K Y E T F S Y L P N F S D E Q L L A Q I D Y L I R S G W V P
Solanum petrophilum F.Muell./Alice Springs N.T.	M Q V W P P I G K K K Y E T F S Y L P T F S D E Q L L A E I D Y L L L S G W V P
Solanum quadriloculatum F.Muell./Alice Springs N.T.	M Q V W P P I N K K K Y E T F S Y L P D F S D E Q L L A E I D Y L L R S G WI/VP
Solanum trilobatum L./P.G.	M Q V W P P I N K K K Y E T L S Y L P D L S D E Q L L L E I D Y L L R S G W V P
Solanum tuberosum L./P.G.	M Q V W P P I N M K K Y E T L S Y L P D L S D E Q L L K E V E Y L L K N G W V P
Solanum violaceum R.Br./P.G.	M Q V W P P I N K K K Y E T L S Y L P D L S D E Q L L K E I D Y L I R S G W V P
Solanum viridifolium Dunal/P.G.	M Q V W P P V G K K K Y E T F S Y L P T L S D E Q L L L E I D Y L I R S G W I P
GROUP 23	

TABLE 2. Continued.

BIGNONIACEAE BIG	
Jacaranda mimosifolia D.Don/Adelaide B.G.	M M V W P T V G L K K F E T L S Y L P D L T S E Q L L K E I E Y L I I K K W I P
Pandorea pandorana (Andrews)Steenis/P.G.	M M V W P T V G L K K F E T L S Y L P D L S S E Q L L K E I E Y L L L K K W I P
GESNERIACEAE GSN	
Saintpaulia ionantha Wendl./P.G.	M K V W P T L G L K K F E T L S Y L P P L S S E Q L I K E I E Y L L L S L L I P
Sinningia speciosa Benth. & Hook./P.G.	M K V W P T V G L L K F E T L S Y L P P L T S E Q L I K E V E Y L L L L G L I P
PEDALIACEAE PED	
Ceratotheca triloba E.Meyer/C.S.	M Q V W P T I G L K K F E T L S Y L P D L T S E E L I K E I D Y L I I N K W I P
Sesamum indicum L./C.S.	M Q V W P P E G K K K F E T L S Y L P D L T S E Q L I K E I D Y L I I N L W I P
SCROPHULARIACEAE SCR	
Digitalis purpurea L./P.G.	M Q V W P P I G L K V Y E T L S Y L P D L T V E Q L A K E I D Y L I I Q K W V P
Paulownia tomentosa (Thunb.)Steudel/Adelaide B.G.	M K V W P T V G L K K Y E T L S Y L P D L T Q E Q L L K E V D Y L I L L K L I P
GROUP 24	
CAPRIFOLIACEAE CPR	
Abelia X grandifolia Rehder/Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L S S A E L A K E V D Y L L R S G W V P
Sambucus nigra L./P.G.	M K V W P I L G L K K F E T L S Y L P P L S E A A L A K E V D Y L L E M G W V P
Viburnum tinus L./P.G.	M K V W P P L G L K K F E T L S Y L P P L S S A Q L A K E V D Y L L E M G W V P
VALERIANACEAE VAL	
Centranthus ruber (L.)DC./P.G.	M K V W P P I N M K K Y E T L S Y L P P L T D E Q L G K E I D Y L I I N K W V P
Valeriana officinalis L./C.S.	M K V W P P I N K K K Y E T L S Y L P P L T R E Q L G K E I D Y L L L N K W V P
GROUP 25	
APIACEAE API	
Apium graveolens L./P.G.	M K V W P P I N L K K F E T L S Y L P P L T T E Q L A K E V D Y L L R S G W V P
Foeniculum vulgare Millan/Kalangadoo S.A.	M K V W P P I N L K K F E T L S Y L P P L T T E Q L A K E V D Y L L R S G W V P
Pastinaca sativa L./P.G.	M K V W P P V N M K K F E T L S Y L P P L T T E Q L A T E V D Y L T T S G W V P
ARALIACEAE ARL	
Fatsia japonica (Thunb.)Decne.& Planchon/Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L S T E Q L A K E V D Y L L K S G W V P
Schefflera actinophylla (Endl.)Harms/Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P P L S T E Q L A K E V D Y L L K S G W V P
INITIALLY UNGROUPED	
ASTERACEAE AST	
Calendula officinalis L./P.G.	M K V W P P L G L K K Y E T L S Y L P P L T E E T L A K E V D Y L L Q N K W V P
Cichorium intybus L./P.G.	M K V W P P L G L K K Y E T L S Y L P P L S E A L L A K E V D Y L L V N K W V P
Eupatorium sordum Less./Adelaide B.G.	M K V W P P L G L K K Y E T L S Y L P T L S E A Q L A K E V D Y L L S S K W V P
Gazania rigens R.Br./P.G.	M K V W P P L G L K K Y E T L S Y L P P L S E A S L A K E V D Y L L R N K W V P
Gerbera jamesonii Bolus/Adelaide B.G.	M K V W P P L G K E K Y E T L S Y L P P L S S E Q L I K E V D Y L L L N K W V P
Helianthus annuus L./C.S.	M K V W P P L G L K K Y E T L S Y L P P L T E E Q L A K E V D Y L L V K K W V P
Lactuca sativa L./C.S.	M K V W P PL/IG L K K Y E T L S Y L P P L S D E A L A K E V D Y L I R N K W V P
Senecio petasitis (Sims)DC./Adelaide B.G.	M K V W P P L G L K K F E T L S Y L P T L S E S Q L A K E V D Y L L S N K W V P
BUXACEAE s.l. BUX	
Buxus sempervirens L./Adelaide B.G.	M Q V W P P V G S K Y F E T L S Y L P P L T T E Q L L A E I D Y L L L S N W V P
Simmondsia chinensis (Link)Schneider/P.G.	M Q V W P P L G S K K F E T L S Y L P P L S P E S L A K E V E Y L L L N G W I P
CAMPANULACEAE CAM	
Canarina canariensis L./Adelaide B.G.	M Q V W P P L G L K K F E T L S Y L P P L S S E E L A K E V D Y L L L S K W V P
Lobelia erinus L./P.G.	M K V W P P L G L K K F E T L S Y L P P L S D E E L A L E V D Y L L L S K W V P

TABLE 2. Continued.

CHRYSOBALANACEAE CHB	
Chrysobalanus icaco L./Lyon Arboretum Hawaii	M K V W P T T G L L K F E T L S Y L P P L T T P Q L A K E V D Y L L L S G W V P
Parinari nonda F.Muell./CSIRO Darwin N.T.	M K V W P T V G K K K F E T L S Y L P P L T T P Q L A K E V D Y L L L T G W I P
CORIARIACEAE CRR	
Coriaria nepalensis Wallich/Melbourne B.G.	M Q V W P P I G L K K Y E T L S Y L P P L S S A E L A K E V D Y L L S K G W V P
CROSSOSOMATACEAE CRO	
Crossosoma californica Nutt./Rancho Santa Ana B.G.	M K V W P P L G L K K F E T L S Y L P P L T P E E L G K E I D Y L L L K G W V P
ELAEAGNACEAE ELE	
Elaeagnus pungens Thunb./Adelaide B.G.	M Q V W P P Y G K K K F E T L S Y L P P L T T E Q L A K E V D Y L L R N G W V P
Shepherdia argentea Nutt./P.G.	M Q V W P P Y G K K K F E T L S Y L P P L T T E S L A K E V D Y L L L N G W V P
EUPHORBIACEAE EUP	
Acalypha wilkesiana Muell. Arg./Adelaide B.G.	M Q V W P P V G S K Y F E T L S Y L P D L T D E S L A S Q V E Y L L L N G W V P
Glochidion ferdinandii Muell. Arg./Adelaide B.G.	M K V W P T F GL/SK K F E T L S Y L P T L S D D Q L A K E V E Y L L L S G W V P
Ricinus communis L./P.G.	M Q V W P PV/LG S K K F E T L S Y L P D L T T E S L A S E V E Y L L L N G W V P
GOODENIACEAE GOD	
Goodenia ovata Smith/Mt Lofty B.G. S.A.	M K V W P P L G L K K Y E T L S Y L P P L D S EE/GL A K E V D Y L L L N K W V P
Scaevola albida (Smith)Druce/Belair S.A.	M K V W P P T G L K K Y E T L S Y L P P L S T D E L A K E I D Y L L L N K W V P
HYDROPHYLLACEAE HYD	
Nemophila menziesii Hook. & Arn./C.S.	M K V W P P E N N K M Y E T L S Y L P D L T T E Q L A K Q I D Y L L I N K W I P
Phacelia tanacetifolia Benth./C.S.	M K V W P P I N L K K Y E T L S Y L P P L T T E Q L A K E V D Y L L I N K W V P
LECYTHIDACEAE LCY	
Couroupita guianensis Aublet/Lyon Arboretum Hawaii	M K V W P P S N N K K F E T L S Y L P N L T D E E L L K E V E Y E L L L G W V P
Lecythis pohlii Berg/Lyon Arboretum Hawaii	M K V W P P S N N K K F E T L S Y L P N L S D E Q L L K E V E Y I L L S G W V P
LOASACEAE LOA	
Mentzelia lindleyi Torrey & A.Gray/C.S.	M Q V W P P I G L K K Y E T L S Y L P P L T T D Q L A K E I E Y L I I S G W V P
NELUMBONACEAE NEL	
Nelumbo nucifera Gaertner/Adelaide B.G.	M Q V W P P T G K K K F E T L S Y L P P L S P E E L A K E V D Y L L L M G W I P
PIPERACEAE PIP	
Peperomia polybotrya Kunth/P.G.	M Q V W P P V G K K K F E T L S Y L P P L T Q E G L L K E I E Y L L I S G W I P
Piper nigrum L./Adelaide B.G.	M Q V W P P E G K K K F E T L S Y L PT/PL S Q E G L A K E I E Y L L M S G W I P
PLUMBAGINACEAE PLB	
Limonium gmelinii Kuntze/Adelaide B.G.	M M V W P P E G L K K F E T L S Y L P P L S S E A L A N E I A Y L I S M T W V P
Plumbago auriculata Lam./Adelaide B.G.	M M V W P P E G K V K F E T L S Y L P P L S S E A L A N E I E Y L L S M T W I P
POLYGONACEAE PLG	
Fagopyrum esculentum Moench/C.S.	M Q V W P P S G K K K F E T L S Y L P P L S E K D L I A Q V N Y L L V K G W V P
Rheum rhaponticum L./P.G.	M Q V W P P E G K L K F E T L S Y L P P L S E A E L L A Q I N Y L L I N G W V P
Rumex obtusifolius L./P.G.	M Q V W P P E G K I K F E T L S Y L P P L S E A D L L A Q I N Y L L I N G W V P

TABLE 2. Continued.

PROTEACEAE PRT	
Adenanthos sericeus Labill./Canberra B.G.	M Q V W P P I N K R K F E T L S Y L L P L S P E A L A K E V D Y L L R K G W V P
Brabejum stellatifolium L./Kirstenbosch B.G.	M K V WP/LPG/LL/GKK K F E T L S Y L P P L S P E Q L A K E V N Y L L L N G W V P
Darlingia darlingiana (F.Muell.)L.Johnson/N.Qld	M Q V W P P L G K K K Y E T L S Y L S P L T S E A L A K E V D Y L L L K G W V P
Embothrium coccineum Forst.et f./Wakehurst B.G. U.K.	M K V W P P L G L K K F E T L S Y L P P L T P E G L A K E V D Y L I R K G W V P
Isopogon latifolius R.Br./P.G.	M Q V W P P V G K K K F E T L S Y L S P L S P E Q L K K E V D Y L L R K G W V P
Knightia excelsa R.Br./Otari B.G. N.Z.	M K V W P P L G L K K F E T L S Y L P P L T S E E L A K E V D Y L L L K G W V P
Leucadendron laureolum (Lam.)Fourc./Adelaide B.G.	M Q V W P P V G M L K F E T L S Y L P P L S S E Q L A K E I D Y L L R K G W V P
Lomatia arborescens L.Fraser & J.W.Vickery/ Canberra B.G.	M Q V W P P V G K K K Y E T L S Y L P P L S S E I L A K E V D Y L L R K K W V P
Lomatia dentata R.Br./Wakehurst B.G. U.K.	M K V W P P L G D K K Y E T L S Y L P P L S S E I L A K E V D Y L L R K G W V P
Macadamia ternifolia F.Muell./Adelaide B.G.	M Q V W P P L G K K K F E T L S Y L P P L T S E Q L A K E I N Y L L I K G W V P
Persoonia chamaepeuce Lhotsky ex Meissner/ Canberra B.G.	M K V W P P K G I P K F E T L S Y L I P L S S E E L A K E V D Y L L L K G W V P
Protea repens (L.)L./P.G.	M Q V W P P V G L K K Y E T L S Y L Q P L S S I E L A K E V D Y L L I K K W V P
Telopea mongaensis Cheel/Canberra B.G.	M K V W P P L G L K K F E T L S Y L P P L T P E I L A K E V D Y L L R K K W V P
Toronia toru (A.Cunn.)L.Johnson & B.Briggs/ Otari B.G. N.Z.	M Q V W P P K G I P K F E T L S Y L P P L S S E E L A K E V D Y L L L K G W V P
RHAMNACEAE RHM	
Ceanothus thyrsiflorus Eschsch./Adelaide B.G.	M Q V W P P L G L K K F E T L S Y L P D L T S D Q L A K E I D Y L I I K G W I P
Rhamnus cathartica L./P.G.	M Q V W P P L G I K K F E T L S Y L P P L T N Q Q L I K E V E Y L I I K G W I P
THYMELAEACEAE THY	
Daphne odora Thumb./P.G.	M Q V W P P V G L K K F E T L S Y L P P L T S E Q L A K E I D Y L I R N K W I P
Pimelea physodes Hook./P.G.	M Q V W P P T N N K K F E T L S Y L P P L S T V Q L A K E I E Y L I R N K W I P
VITACEAE VIT	
Parthenocissus quinquefolia Planchon/P.G.	M K V W P T E G L I K F E T L S Y L P P L S S E E L G K E V D Y L L L K K W V P
Vitis vinifera L./Adelaide B.G.	M K V W P T E G L M K F E T L S Y L T P L S Y E Q LA/RK E V D Y L L L K K W I P
MONOCOTYLEDONS	
ALISMATACEAE ALI	
Sagittaria graminea Michaux/Adelaide B.G.	M K V W P V E G L K K F E T L S Y L P P L T T E Q L L K Q I E Y L L R N G W I P
APONOGETONACEAE APG	
Aponogeton distachyos L.f./Mylor S.A.	M Q V W A P E G L K K F E T L S Y L P P L T S E Q L L K E V D Y L I I K G W I P
ARACEAE ARA	
Arum maculatum L./P.G.	M Q V W P P E G L K K F E T L S Y L P P L S D E A L A K E V D Y L I I K G W I P
Philodendron giganteum Schott/P.G.	M Q V W P P L G L K K F E T L S Y L P P L S N I N L S K E V D Y L L L N G W I P
ARECACEAE ARE	
Brahea armata S.Watson/Adelaide B.G.	M K V W PI/VE G LA/KK F E T L S Y L P P L S I E A L L K Q I E Y L L L S G W V P
Chrysalidocarpus lutescens (Bory)Wendl./ Adelaide B.G.	M K V W P I E GH/KK K F E T L S Y L P P L P I E A L L K Q I E Y L L L S G W I P
COMMELINACEAE CMM	
Commelina coelestis Willd./P.G.	M K V W P I E G V K K F E T L S Y L P P L T P E I L L K Q V D Y L L L S G W V P
Rhoeo discolor Hance/P.G.	M K V W P I E G K K K F E T L S Y L P P L S N T I L L K Q I D Y L I L S K W V P
LILIACEAE s.l. LIL	
Asparagus falcatus L./Adelaide B.G.	M K V W P I A G K K K F E T L S Y L P P L S I E Q L I K Q I E Y L I L S S W I P

TABLE 2. Continued.

Aspidistra elatior Blume/Adelaide B.G.	M Q V W P I E G V K K F E T L S Y L P P L S I E Q L I K Q I D Y L L R N G W I P
Liriope spicata Lour./Adelaide B.G.	M K V W P I E G M K K F E T L S Y L P D M T T V Q L I K K I E Y L L L N K W I P
Ruscus hypophyllum L./Adelaide B.G.	M K V W P I E G V K K F E T L S Y L P D M T I E Q L I K Q I E Y L I K N K W I P
ORCHIDACEAE ORC	
Cymbidium X floribundum Lindley X C.lowianum (Reichb.f.)/see ref. G.C.Martin	M Q V W P I E G V K K F E T L S Y L PT/PL ST/PE A L L K Q I D Y L L R S G W I P
POACEAE POA	
Hordeum vulgare L./C.S.	M Q V W P I E G I K K F E T L S Y L P P L S T E A L L K Q V D Y L I V K K W V P
Lolium perenne L./C.S.	M Q V W P I E G I K K F E T L S Y L P P L S A E A L L K Q I D F L I R K K W V P
Phragmites australis (Cav.)Trin. ex Steudel/ River Torrens S.A.	M Q V W P I E G I K K F E T L S Y L P P L T T E D L L K Q I E Y L I V K K W I P
Piptatherum miliaceum (L.)Cosson/P.G.	M Q V W P I E G I K K F E T L S Y L P P L S V E AL/FL K Q I E F L I V K K W V P
Triticum vulgare L./C.S.	M Q V W P I E G I K K F E T L S Y L P P L S T E A L L K E V D Y L I V K K W V P
SMILACACEAE SML	
Eustrephus latifolius R.Br./Canberra B.G.	M K V WP/IP/IEG M K K F E T L S Y L P D L S V E Q L I K Q I E Y I L I N K W V P
Geitonoplesium cymosum (R.Br.)A.Cunn. ex Hook./ Canberra B.G.	M K V W P I E G L K K F E T L S Y L P P L T V D Q L L K Q I D Y I L I S K W I P
G Y M N O S P E R M S	
EPHEDRACEAE EPH	
Ephedra fragilis Desf./Adelaide B.G.	M L V W P N K D N I K F E T L S Y L P T L S Q E A L I K Q I D Y L L L S K W V P
GINKGOACEAE GNK	
Ginkgo biloba L./P.G.	M Q V W N P Y N N K K F E T L S Y L P P L S P E G L L K E I D Y L L N N G W V P
CYCADACEAE CCD	
Macrozamia communis L.Johnson/Bateman's Bay N.S.W.	M Q V W P P Y N N K K F E T L S Y L P P L S K P Q L L L E I D Y L L G N K W I P
TAXODIACEAE TXO	
Metasequoia glyptostroboides Hu&Cheng/Adelaide B.G.	M Q V W P P Y N N K K W E T L S Y L P P L S P E Q I L K Q V I Y I L K N K W V P
WELWITSCHIACEAE WLW	
Welwitschia mirabilis Hook.f./C.S.	MQ/LV W P N KG/NL L K F E T L S Y L P D L T P E Q L L K Q I D Y L L L N K W V P

angiosperm ancestors. All three members of Acanthaceae that were tried failed with symptoms like these, as did four out of six species from Caesalpiniaceae.

Finally, an entirely different sort of failure occurred with four species, all hemiparasites from the putatively related families Santalaceae and Loranthaceae. These species had abnormally high amounts of phenolics, but it seems unlikely that failure can be attributed to them or to any of the other causes mentioned above. The preparations always yielded abnormally high amounts of plastocyanin but no trace of rubisco-SSU. Plastocyanin, a chloroplast protein, has a molecular weight sufficiently close to rubisco-SSU that it occurs, occasionally, as a small contaminant detected during sequencing. It could be identified by its sequence but, except in these two families, it was so weak that it disappeared after about seven positions. The strength of the plastocyanin sequence in all four of these hemiparasites suggests that the absence of rubisco-SSU could not be ascribed to some general difficulty like proteases, but might reflect an unusual, perhaps facultative, photosynthetic system.

General Remarks about the Sequences

overall variation and invariant sites

A summary of the variation that we have observed is given in Table 3; the amino acids most commonly observed are in the top line.

The rubisco-SSU gene includes two introns, the first of which is inserted before the codon that determines amino acid 3. It determines valine and this, like tryptophan at position 4, is invariant, the two codons carrying the signal to cut the end of the intron (Berry-Lowe et al., 1982). These invariant residues were useful early signals that the correct protein fraction had been chosen. Within the first 40 amino acids, proline always occurs at position 5 and/or 6, at position 19 and/or 20, and at position 40. These three regions correspond to bends in the tertiary structure of the molecule. Chapman et al. (1988) have indicated that between the first and second bend there is alpha-helix and thereafter beta-sheet. There is an almost invariant region from amino acids 13 to 18, a region that makes contact with one of the large subunits (Chapman et al., 1988; Knight et al., 1989). The only variation we have found in this region is the substitution of phenylalanine for leucine at position 15 in five species of *Solanum* (Martin et al., 1986). These same species also have phenylalanine substituted for leucine at the almost invariant position 21. The simultaneous occurrence of two very rare substitutions indicates a causal connection. Hydrophobic bonding between the two positions may stabilize the bend at position 19 and, because these species are inhabitants of very hot and arid regions, this may have been a factor in natural selection.

Heterogeneity within species

The first reports of rubisco-SSU sequences (Strobaek et al., 1976) were for the N-terminal amino acids in species of *Nicotiana*, and these showed heterogeneity at positions 7 and 8 in tobacco. We have also found it at position 30. These heterogeneities are undoubtedly associated with the amphidiploid origin of tobacco and led to the expectation that heterogeneity would be fairly common, not only because about one-third of plant species are polyploid, but also because in diploids gene duplications are frequent. We may not have detected some heterogeneities (for example, those involving serine, which gives a weak signal), but we did detect 34 species with one heterogeneity, 11 with two, and 4 with three. The demonstration by Pichersky et al. (1986) that in tomato there were at least three different DNA messages for rubisco-SSU, all with the same N-terminal amino acid sequence, suggests that selection acts strongly to preserve primary amino acid structure. There are at least eight different genes encoding rubisco-SSU in petunia (Lamb & Fitzmaurice, 1986); for this reason, when we prepared protein from that species, we used a mixture of equal quantities of leaves from four morphologically different varieties, with the aim of finding heterogeneities (Martin & Dowd, 1984b). The sequence was of high quality but no heterogeneity was detected. Likewise, we chose to study *Rhoeo discolor* because it is a complex interchange heterozygote for all chromosomes and might therefore be heterozygous for rubisco-SSU, but we detected no heterogeneity. Heterogeneities that were found presented no problem for the computer analysis.

INSERTIONS

Only two examples of additional amino acids in the N-terminal sequence have been found. Both species of Epacridaceae that we studied had an additional isoleucine between normal positions 9 and 10. *Teucrium flavum* (Lamiaceae) had two additional glycines, probably between the same two positions. These insertions, while clearly of taxonomic significance, have been ignored during data processing.

THE N-TERMINUS

Haslett et al. (1976) reported that the N-terminus of rubisco-SSU was "frayed," some molecules seeming to have methionine in position 1 while others are without it. This is the situation that we have encountered in the vast majority of species, the effect being that at every position two amino acids are recorded, the correct one and the next one. Usually the two signals are approximately equal, especially when the protein is of highest quality. This property is helpful in that it provides a second opportunity for identification and is useful for identifying minor contaminating proteins whose residues appear only once, but probably means that it is more difficult to obtain long sequences because attenuation of the signal occurs earlier.

All those species for which nucleic acid sequences have been reported were also studied by us and all show fraying. Because the nucleic acid sequences show the N-terminus to be methionine, there is no doubt. The signals we obtained were not typical for either methionine or its sulfone derivative. Whether the derived amino acid is obtained by dansylation (in manual sequencing) and identified by TLC, or is the PTH derivative from automatic sequencing and identified by HPLC or TLC, the N-terminal amino acid moves differently from methionine; therefore, we conclude that it is a modified form of that amino acid.

Two exceptions to the above generalization have been encountered. In 10 out of 11 species of the Onagraceae the N-terminus is phenylalanine, the only variations from methionine known, and in these there is no sign of fraying. In six other species the N-terminal amino acid is methionine (and gives the normal signal for PTH-methionine), but there is no sign of fraying, the difference from the majority of species being sharp and unmistakable; these are two members of Papaveraceae (*Papaver orientalis* and *Eschscholtzia californica*), two from Pedaliaceae (*Sesamum indicum* and *Ceratotheca triloba*), *Vitex lucens* (Verbenaceae), and *Mentzelia lindleyi* (Loasaceae). Any hypothesis to explain fraying must account for these exceptions, and we believe that they exclude artifacts arising from techniques of protein production or sequencing. Any hypothesis must also account for the modification of methionine and the equality of the two forms of the protein. We therefore dismiss as unlikely hypotheses relying on inefficient shortening of the protein either as it passes through the chloroplast membrane or after entry.

It is known that rubisco-SSU forms dimers (Roy et al., 1978), and we suggest that this may be through formation of disulphide bridges between the N-terminal methionines of two SSU molecules. This might occur in vivo if the enzyme model of Chapman et al. (1988) is correct, but is more likely an in vitro event if the different model of Knight et al. (1989) is correct. If dimers are formed, S-carboxymethylation at pH 8.6 would not break an inter-methionine bond, but we suggest that the dimer does fall apart so that dimethionine is on one chain and no methionine on the other. This hypothesis would account for all phenomena except for non-fraying species, which presumably do not naturally form dimers.

Methods of Data Analysis

Before computer analysis, amino acid sequences were converted to inferred nucleotide sequences using the genetic code. Usually this could be carried out after inspection of, for example, all the sequences in a Group so that the most parsimonious choices of codons could be made. A standard was chosen at sites where substitution was silent. Although a program was available (Martin et al., 1983), usually the path was obvious and computing unnecessary. Thus the unit of length in phylogenetic trees is an inferred nucleotide difference (i.n.d.).

The number of dichotomizing trees (phylogenetic Steiner trees) connecting N taxa is $1 \times 3 \times 5 \ldots (2N-5)$. The principle of analysis is that the length of every possible tree is calculated and the shortest tree is chosen as the most probable. This agrees with the parsimonious hypothesis that evolution has proceeded by the shortest route. However, because the total number of possible trees increases very rapidly, i.e., when increasing from N-1 to N taxa it increases (2N−5)-fold, it is not always possible to consider every tree.

Except during the final stages of this project, the program that we used was MINTREE, the "branch and bound" program of Hendy and Penny (1982). With a Vax 785 computer the usual limit for simultaneous analysis was 12 taxa. This limit could be extended to about 15 with a supercomputer (Cyber 205), but the trouble and expense precluded useful work. Although MINTREE has now been superseded, its co-program ANALYZE is still used because it possesses efficient routines for obtaining ancestral sequences and internodal lengths.

Most of the analyses have been carried out using HENNIG86 (Farris, 1988) and a personal computer (Microbyte 230). This system is about two

TABLE 3. Summary of N-terminal sequences of RUBISCO-SSU from 136 families of seed plants. The number under an amino acid indicates in how many families it is found. For key to amino acid symbols see Table 2.

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
M	Q	V	W	P	P	L	G	L	K	K	F	E	T	L	S	Y	L	P	P	L	S	S	E	Q	L	A	K	E	V	D	Y	L	L	L	S	G	W	I	P
136	75	136	136	132	114	68	124	98	129	131	117	136	136	136	136	136	136	132	108	136	95	47	115	95	136	81	128	121	103	100	135	133	117	85	62	100	130	86	136
F	K			N	T	V	N	K	L	Y	Y			F				S	D	M	T	T	A	E	I	L	A	Q	I	E	F	I	I	I	K	K	L	V	
1	73			3	28	32	23	47	10	4	29			2				5	36	3	75	45	19	50	3	52	9	28	57	55	6	7	49	35	61	44	6	85	
	M			A	I	E	D	N	I	I	W							L	T	F	V	P	Q	A	F	I	L	K	R	N		E	T	R	N	N	S		
	9			1	8	30	2	12	7	2	1							2	16	1	3	32	17	20	1	21	5	2	1	8		1	1	30	48	7	2			
	L			E	V	I	V	M	R	L								I	E	I	D	D	D	S		G	R			A				S	M	S	G			
	8			1	4	24	2	9	4	2								1	4	1	2	23	10	15		12	2			3				15	8	3	1			
	A			I	N	T	A	I	Q	E								Q	S	V	N	E	K	G		S	G			Q				K	Q	L				
	1			1	2	15	1	5	3	1								1	4	1	2	18	4	5		4	1			3				14	4	2				
	E			L	S	Y	E	V	V	M								T	N		P	Q	V	D		T	N			I				N	L	T				
	1			1	2	11	1	5	3	1								1	3		1	16	4	3		2	1			2				12	3	2				
	N			Q	F	E	L	Y	P	T									Q			V	I	I		K	Q			F				V	V					
	1			1	1	8	1	4	2	1									2			10	3	3		1	1			1				6	3					
	S			Q		S	L	S	A	V												A	I	N		R	S			G				A	T					
	1			1		7	1	3	1	1												9	3	2		1	1			1				2	2					
	T			S		K	T	D	S													N	P	L			T			S				E	E					
	1			1		5	1	2	2													8	3	1			1			1				2	1					
						A		G	E													I	P	T										G	R					
						2		1	1													4	3	1										2	1					
						F		P	M													K	I											Q						
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orders of magnitude faster than the above and has the additional advantage that an analysis can be left running for days or weeks. The principles of its algorithms have not been published, but the time of its release suggests a possible connection with a published letter by Johnson (1987). HENNIG86 offers a number of options, which comparison with MINTREE using the same sets of data suggest are reliable; in order of preference we have used implicit enumeration (*ie**); *ie* followed by *bb* (branch swapping); *mhennig* followed by *bb*. Beyond the number of taxa that can be handled by MINTREE or the *ie* option of HENNIG86, correct solutions cannot be guaranteed.

A further advantage of HENNIG86 is that it includes a program for successive weighting, which often reduces the result to one or very few trees. This usually eliminates the need to derive consensus trees, a process that we have found unsatisfactory (Martin & Dowd, 1989). Finally, HENNIG86 derives the *ci* (consistency index) (Carpenter, 1988) and *ri* (retention index) which we record with each figure of a tree. In a personal communication, Farris defines these as follows: if r and m denote, respectively, the smallest and greatest number of steps that a character can require on any tree, and s denotes the number of steps that character requires on a considered tree, then c.i. is r/s and r.i. is (m-s)/(m-r).

MINTREE uses data such that each of the four nucleotides is entered as 1, 2, 4, or 8, which allows the counting of ordinary differences and also of heterogeneities; no matter what variation occurs at a site, it can be recorded as a sum that is always different for different combinations. Provided there are no heterogeneities, HENNIG86 can use the same notation (using the nonadditive option); if there are heterogeneities, they must be recorded by inserting additional taxa. This is satisfactory if there is only one variable site within a taxon when only two taxa need to be recorded. Assumptions of linkage must be made, however, if there is more than one variable site but only two taxa are to be recorded. This problem becomes increasingly important as an analysis progresses from using raw data to derived ancestral sequences for families and then Groups because, in these, heterogeneities may be numerous. We have therefore used alternative strategies. The first is inserting additional taxa as just described and accepting the result if the different versions of a taxon cluster without interruption.

The second strategy is to use binary coding for nucleotides; e.g., 1000 for A, 0100 for G, 1100 for A and G, 0010 for C, and so forth. In conjunction with HENNIG86, MINTREE notation is slower than binary notation, which is therefore advantageous. As would be expected, binary gives a tree length double that using MINTREE notation but it is seldom exact. If inexact, the length is always less than double, and there is a loose relationship between the deficit and the number of heterogeneities. Because the details of HENNIG86 have not been published, we have been cautious about choosing between these alternatives and have done all Group analyses with HENNIG86 using both notations.

We structured our investigation such that the majority of families were represented by at least two species from different genera. If we accept that taxonomy is seldom wrong when placing genera within families (Heywood, 1978), then we have an empirical way of judging the merits of the two notations. Omitting families that have either a single representative or are multiply represented, all Groups have been analyzed using both notations and, from the minimal trees recorded, we have chosen the best as judged by pairing of representatives of families. In eight Groups both methods had the same best tree, in six binary gave the best, and in eleven MINTREE notation gave the best. In the section "Analyses Within Groups" we have therefore used the taxonomically best minimal tree no matter which notation was used to derive it. However, in later sections we have used binary notation exclusively because it is quicker and more convenient.

Among best trees, 79% of families showed correct pairing of its members. When judging this result, it should be remembered that a single misplaced species will often result in the failure of pairing of representatives of two families. While a few such occurrences may be the result of incorrect taxonomy, the remainder are presumably caused by convergent evolution. The details can be seen in the figures for the Groups.

Analyses within Groups

Explanation of the figures

The figures are drawn to scale, which is indicated by the length of one inferred nucleotide difference (i.n.d.). Only lengths have meaning, not angles. Usually at least two trees have been derived for each Group, one using sequences of individual species and the second using derived familial nodes. If the first shows congruent grouping of putative members of families, then the second is not needed.

Disruption of familial grouping is often caused by the sole representative of another family or by a member of a multiply represented family. The second tree is derived from familial nodes and singletons, is drawn with a different scale, and uses only the three-letter familial abbreviation of Weber (1982), which is given in Table 2. When appropriate, trees of multiply represented families or genera are also given. In later analyses, Group nodes, and often one or two others, will be used; each of these is numbered.

The Base of the Angiosperm Tree

Before detailed analysis of Groups began, many analyses were done using the five gymnosperms, representatives of the monocotyledons and of Groups 1, 2, and 3 which were most likely, on taxonomic grounds, to be near the root of the dicotyledon tree. The angiosperm family closest to the gymnosperms was Schisandraceae. Figure 1 shows the junction of the gymnosperms, Schisandraceae, and the other angiosperms. The derived sequence of this node has been used as "Base" in all subsequent Group analyses.

It will be noted that Figure 1 is different from, and taxonomically more satisfactory than, the equivalent figure of Martin and Dowd (1989). Since then a sequence of *Welwitschia* has been obtained and this paired with *Ephedra* between the angiosperms and the other gymnosperms. Three attempts to study *Gnetum* were made but all failed with symptoms suggesting strong leaf protease activity.

Group 1. An attempt to study *Hedycarya* (Monimiaceae) having failed, *Peumus* was left as a singleton, which was therefore omitted from Figure 2a but included in Figure 2b. Correct pairing and grouping occurs in all families except Aristolochiaceae for which a derived familial node is shown in Figure 2b. As indicated above, Schisandraceae is nearest to Base with a rather long gap to the remainder.

Group 2. In contrast to the straightforwardness of the previous Group, Group 2 has presented problems that arise from the great intrafamilial variation of Ranunculaceae and Papaveraceae, the trees for which are shown in Figure 3b and c. The two derived familial nodes are shown with the rest of the Group in Figure 3a. We interpret Ranunculaceae and Papaveraceae to be ancient angiosperm families, and only with some misgivings have we adhered to our acceptance of current taxonomy at the levels of family and below. This is especially so for Papaveraceae, but splitting off Fumariaceae creates more problems than it solves.

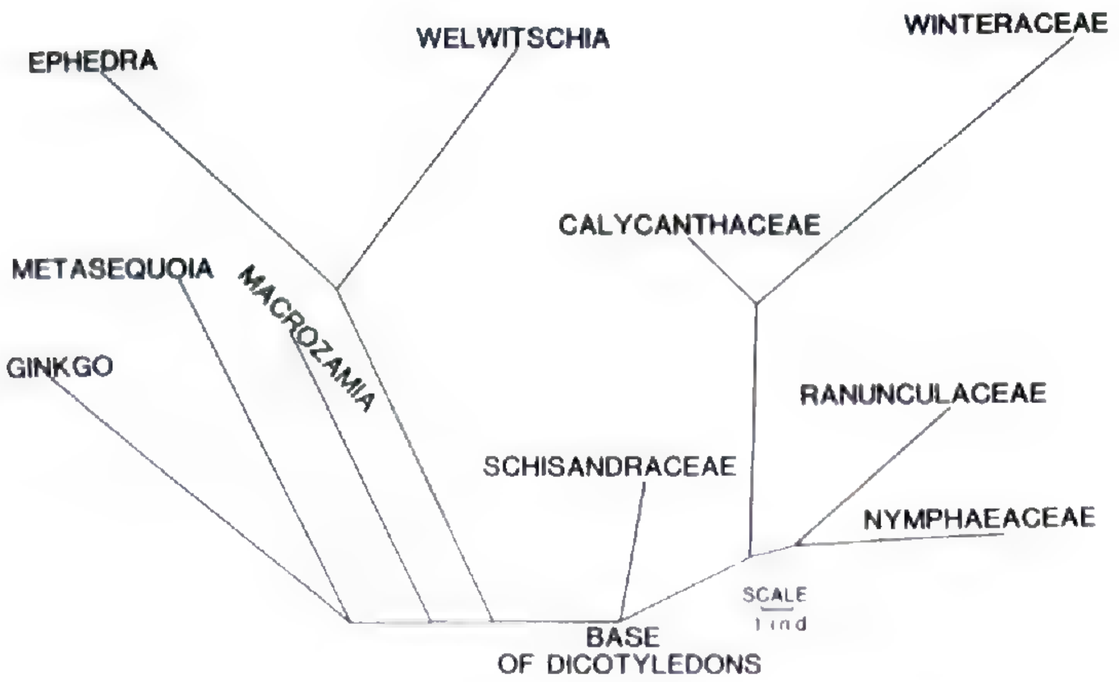


FIGURE 1. Five gymnosperms analyzed with familial nodes of five angiosperm families from Groups 1, 2, and 3. The ancestral sequence derived for the junction of Schisandraceae has been used as an outgroup for analyzing the Groups of dicotyledons.

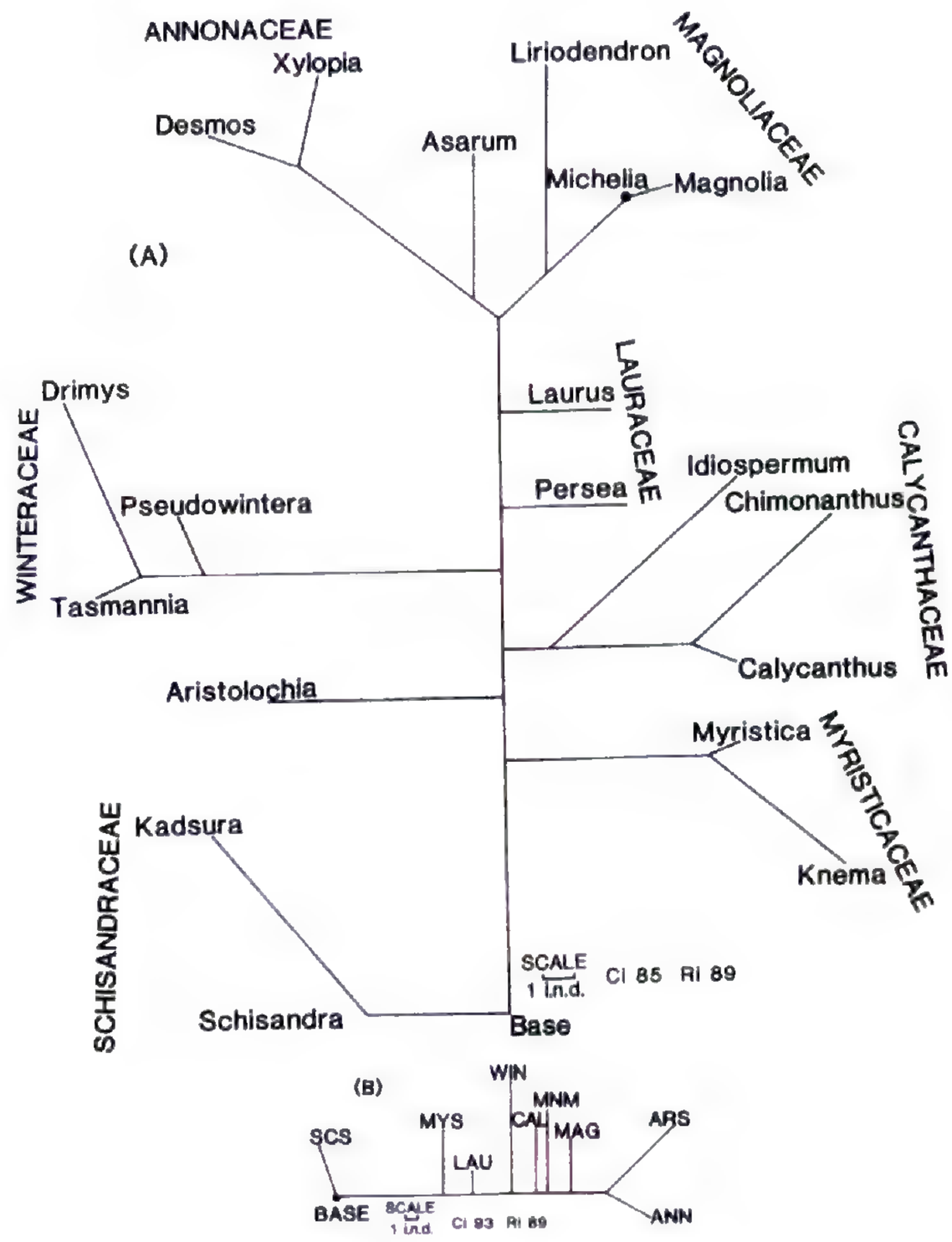


FIGURE 2.—(A). Group 1, omitting the single representative of Monimiaceae.—(B). Tree of family nodes for Group 1.

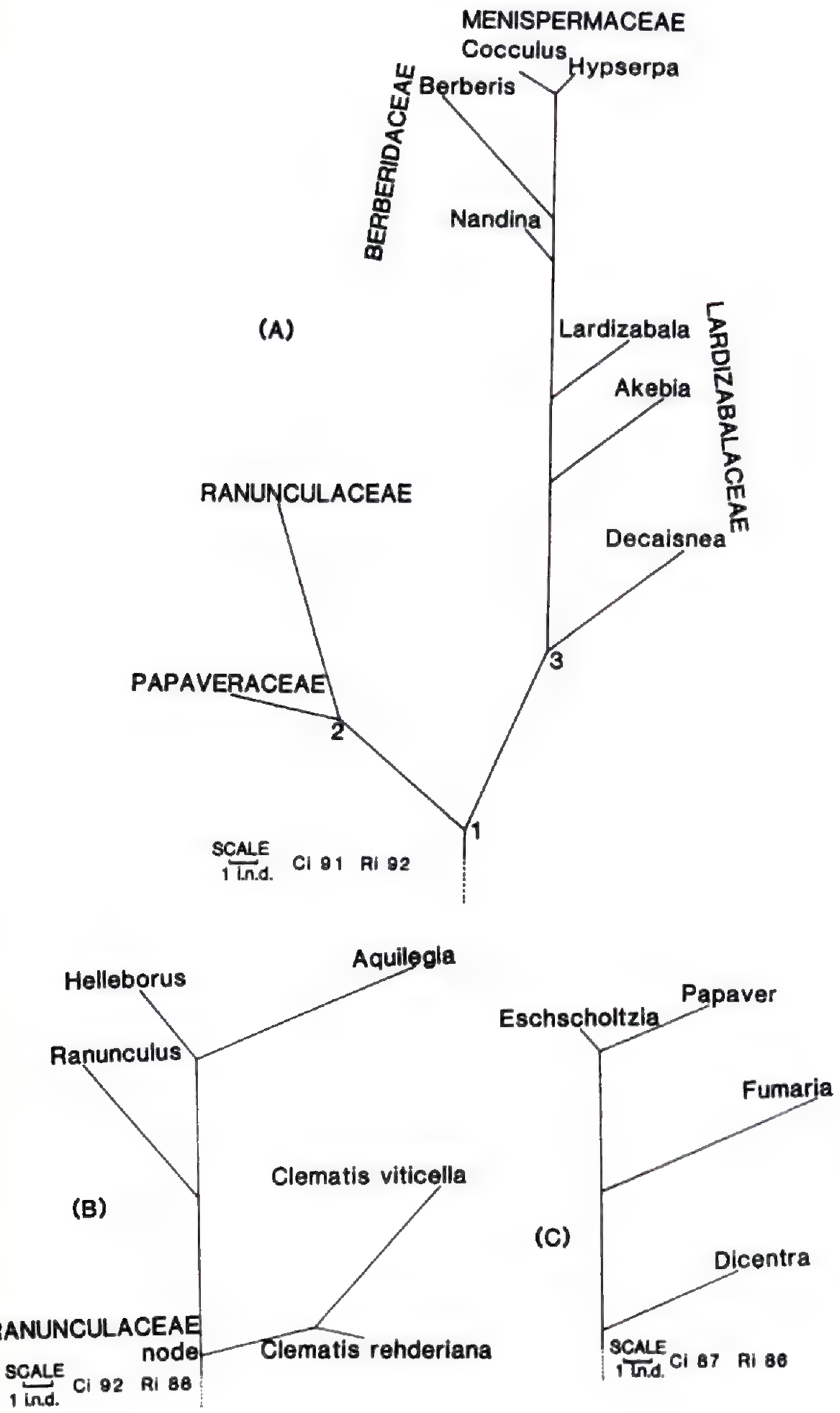


FIGURE 3. (A) Group 2, with family nodes, derived from (B) and (C) for Ranunculaceae and Papaveraceae s.l.

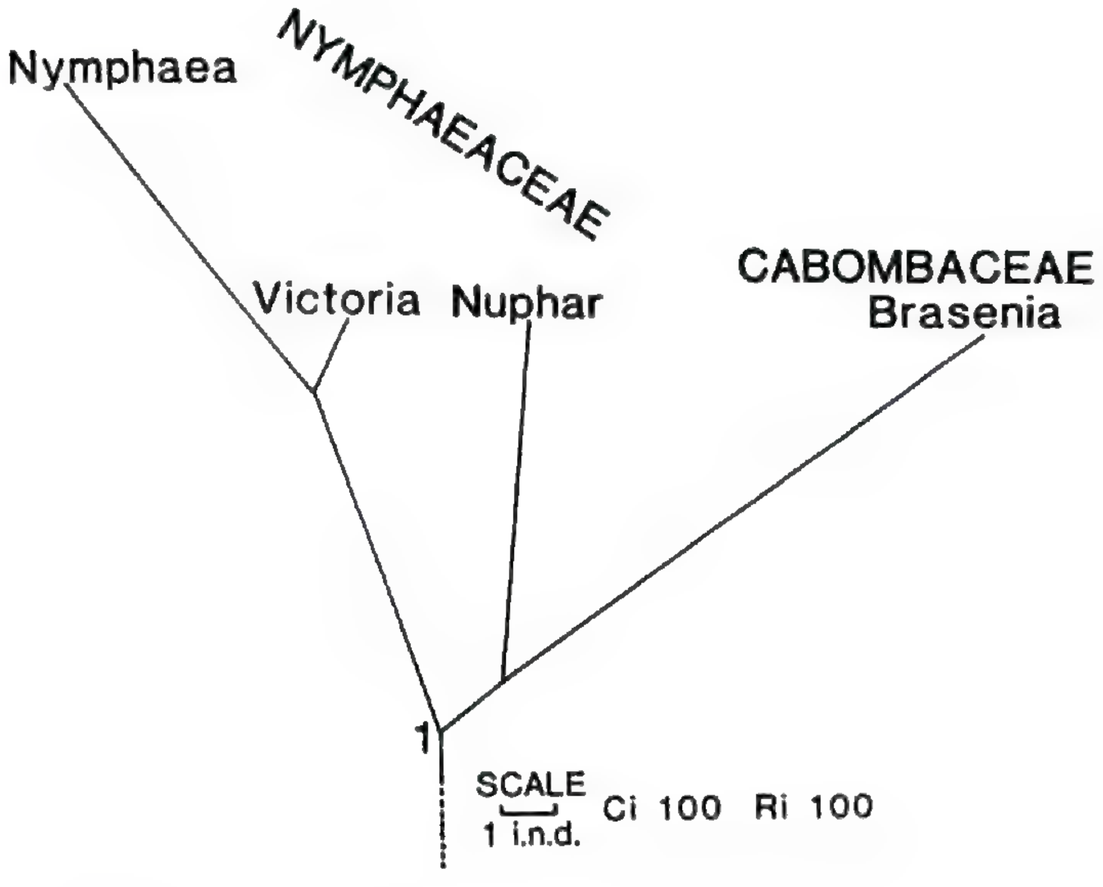


FIGURE 4. Group 3.

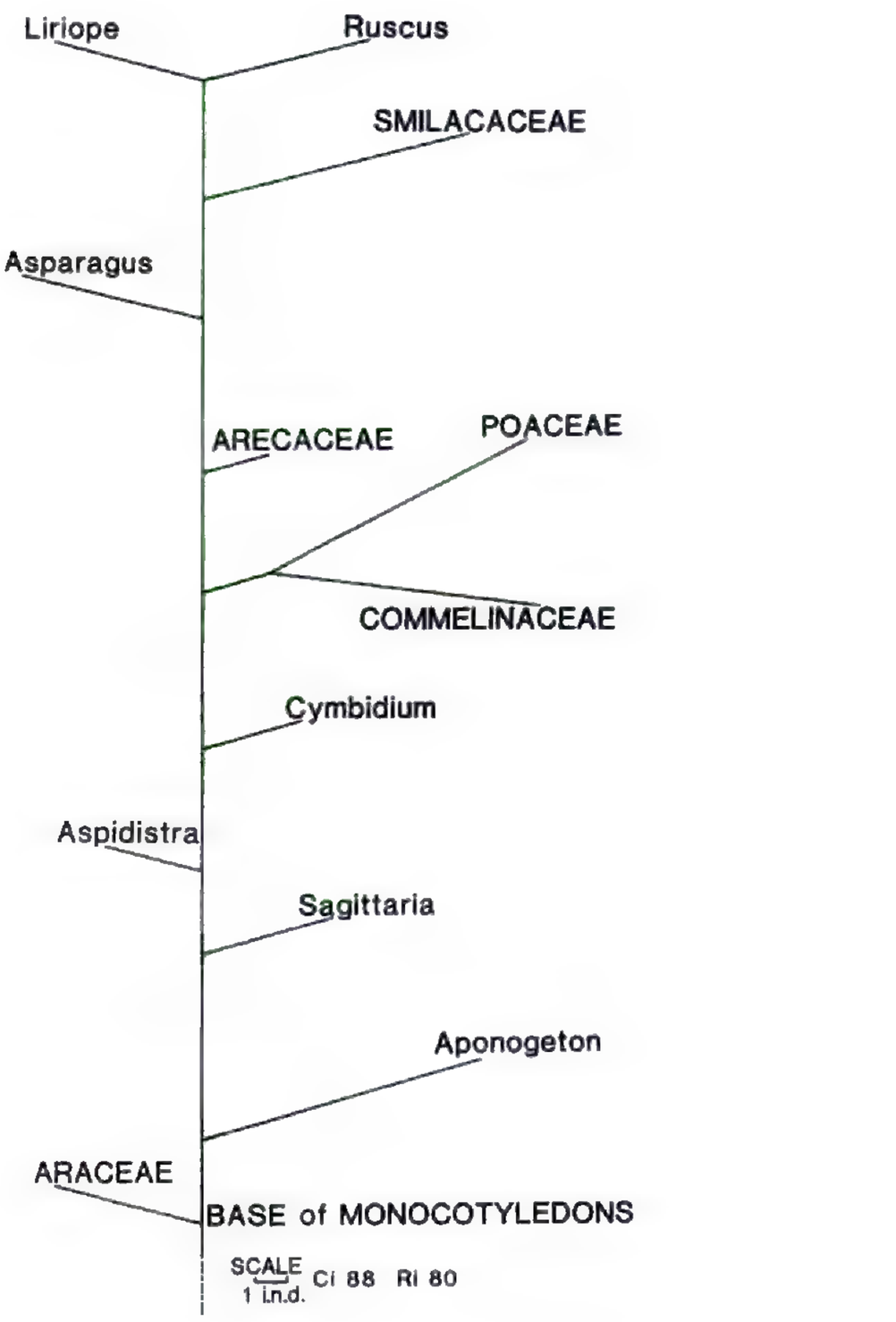


FIGURE 5. The monocotyledons that have been studied with some families represented by their nodes.

Group 3. Failure with a species of *Cabomba* has left *Brasenia* as a singleton that does not separate from the three members of Nymphaeaceae; however, the internode is so short that we draw no significance from it (Fig. 4).

Piperaceae, Nelumbonaceae, and the monocotyledons. Piperaceae and Nelumbonaceae have not been placed in a Group because in both cases opinions differ among the four phylogenies considered when we nominated Groups. All place them in either our Group 3 or Group 1, so it is appropriate to carry out a joint analysis with the members of these two Groups, and at the same time to consider the links with the monocotyledons. Although no species have been added to those reported earlier (Martin & Dowd, 1989), the sequences have been reanalyzed with HENNIG86. To reduce the number of taxa to be compatible with the *ie* option, familial nodes have been used for Araceae, Arecaceae, Commelinaceae, Poaceae, and Smilacaceae (Fig. 5). The monocotyledon node has been derived and is included in Figure 6. The result is different from that of Martin and Dowd (1989), and this is presumably because of the new computing program.

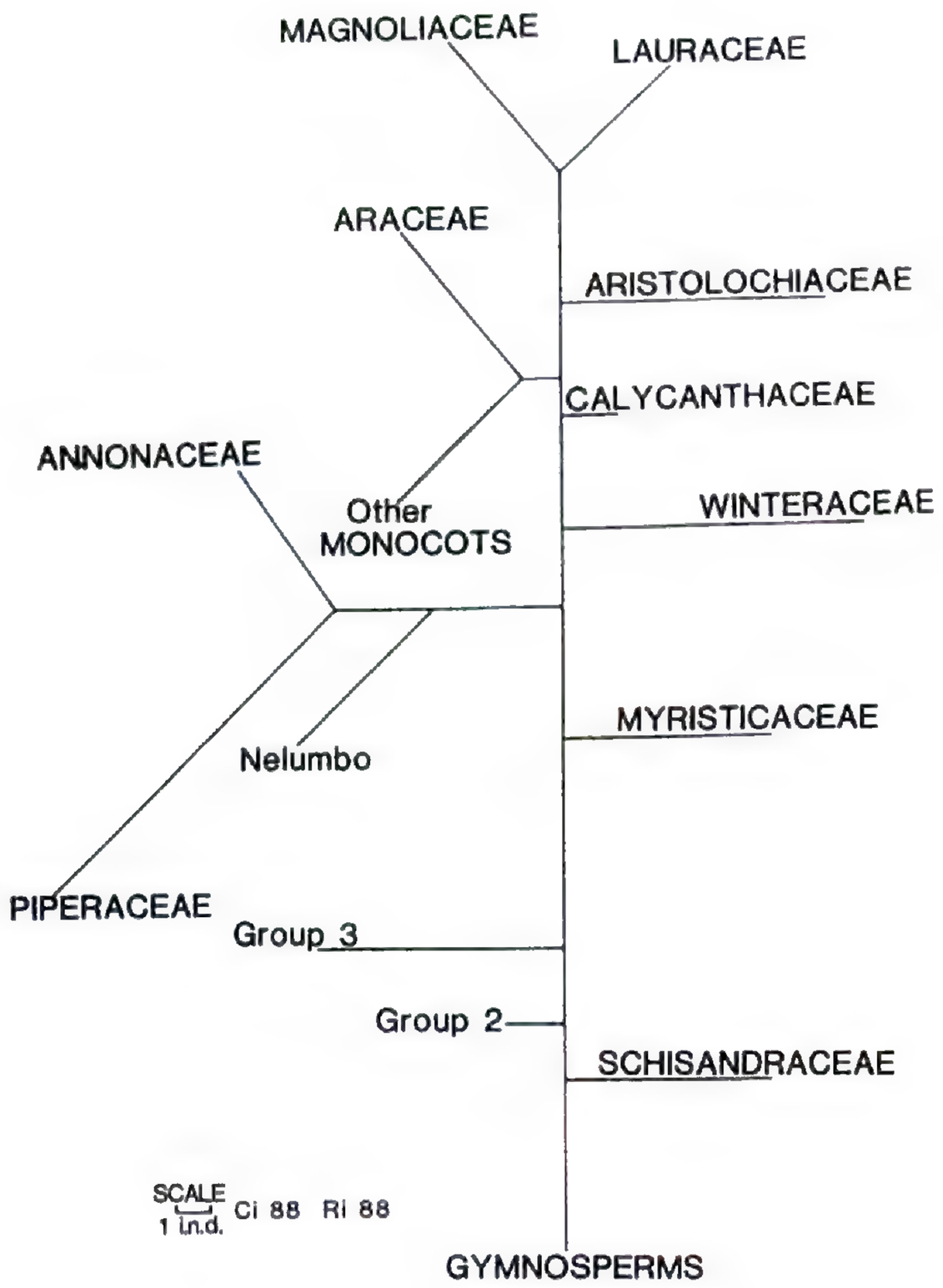


FIGURE 6. The base of the angiosperm tree showing the relationship of the monocotyledons to members of Groups 1, 2, and 3 and *Nelumbo* and Piperaceae.

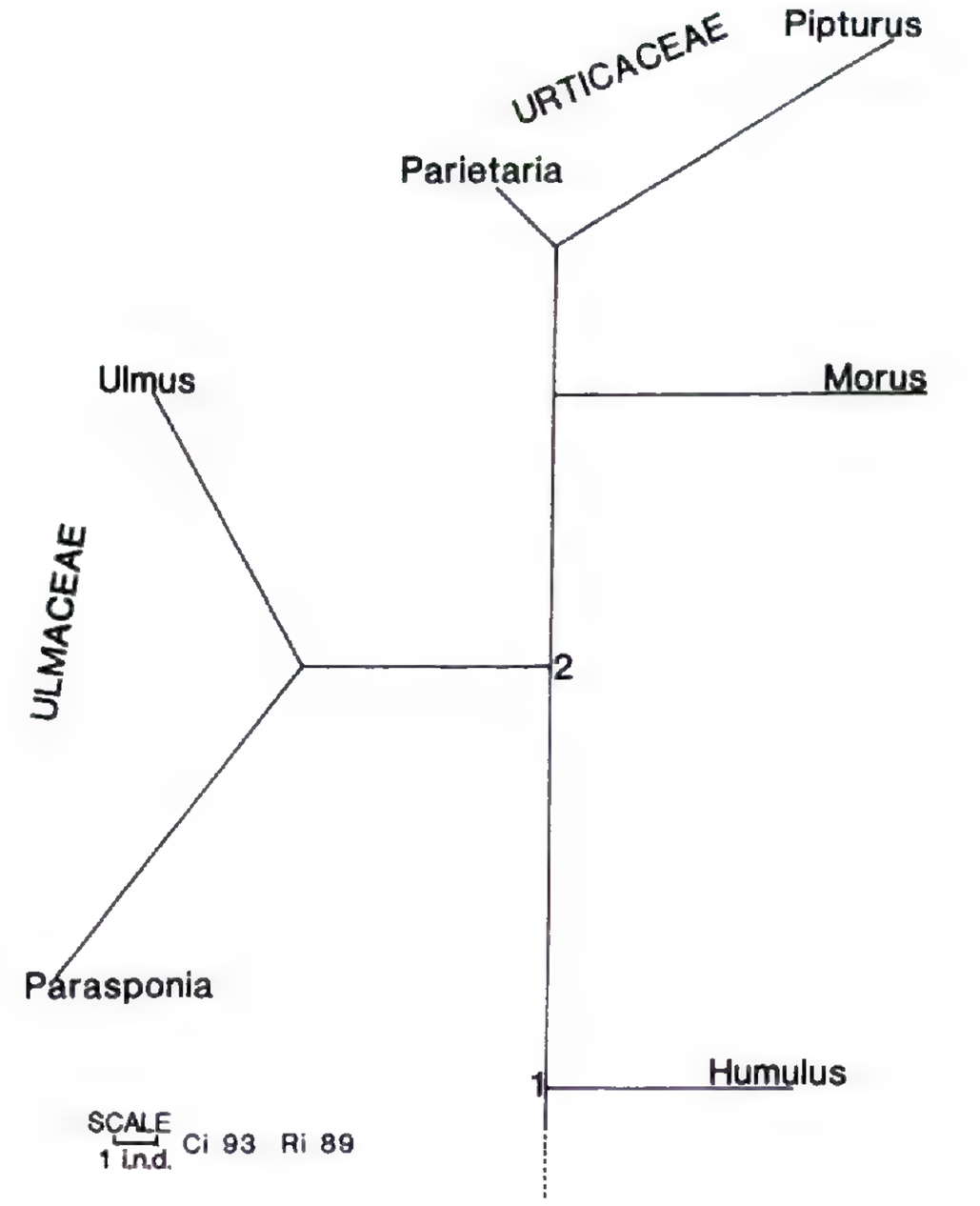


FIGURE 7. Group 4.

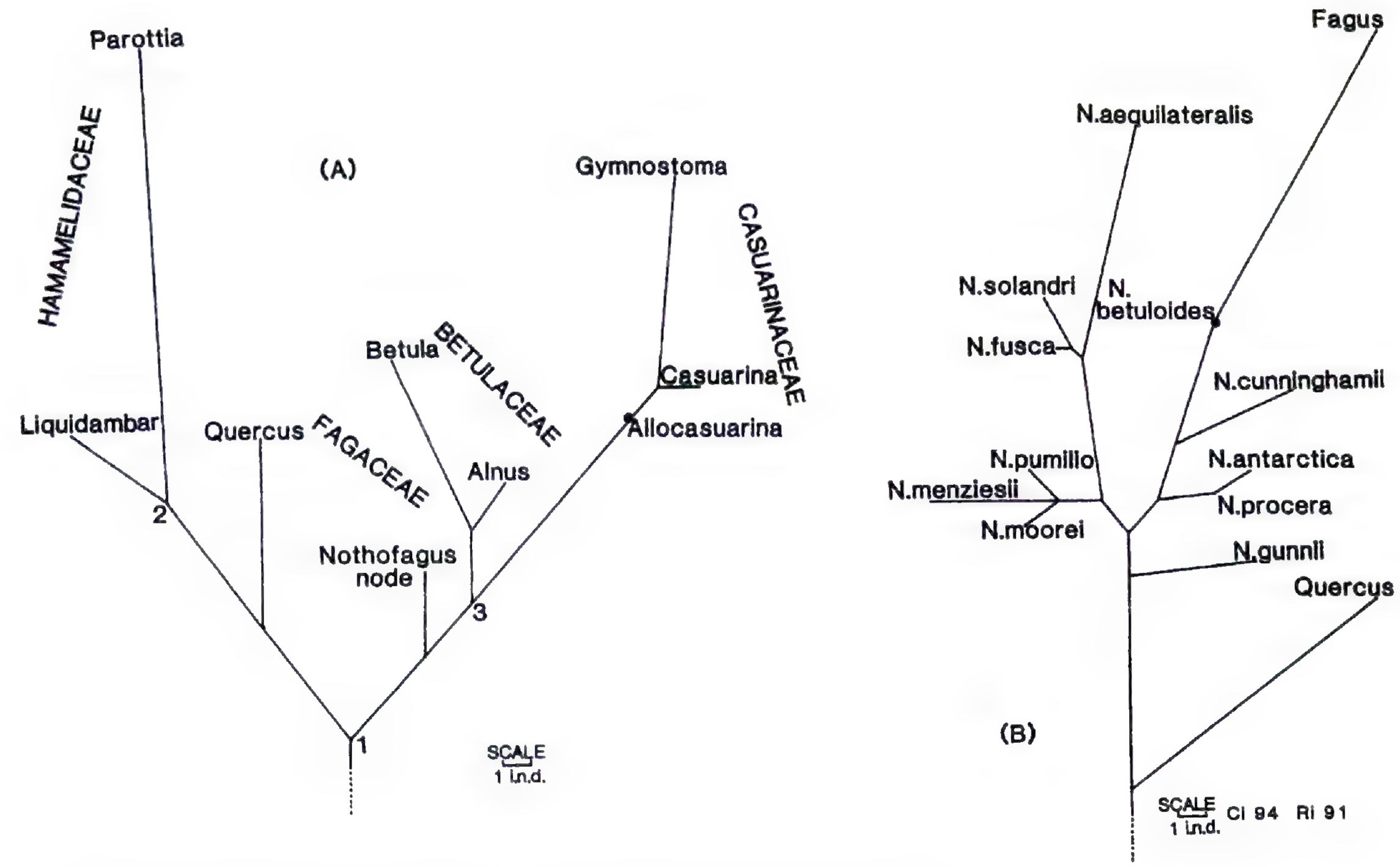


FIGURE 8.—(A). Group 5. The node for *Nothofagus* was derived from (B).

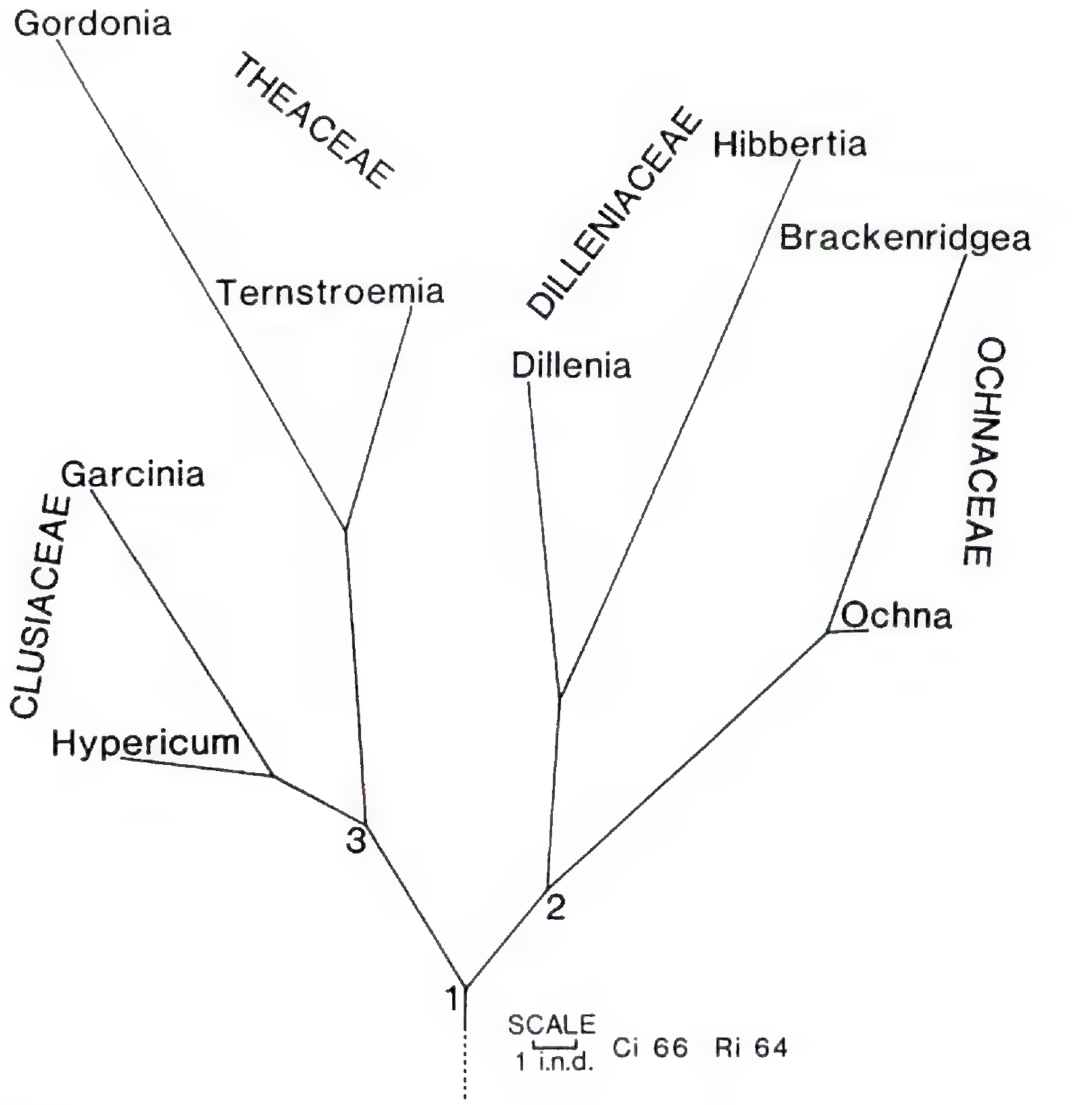


FIGURE 9. Group 6.

Group 4. There is good pairing between members of Ulmaceae and Urticaceae but not Moraceae (Fig. 7). It was only after failures with two species of *Ficus* and one of *Maclura*, almost certainly due to protease activity, that we supplemented with *Humulus*, knowing that its taxonomic position was not entirely clear. The failure of *Humulus* and *Morus* to pair was therefore not surprising. Subsequently, *Humulus* was removed from Group 4 and added to the list of uncertain taxa (see below).

Group 5. The tree of *Nothofagus* (Fig. 8b) is slightly different from that of Martin and Dowd (1988) because it is influenced by the weighting procedure of HENNIG86 and because it includes *Fagus*, which does not separate. From this tree a node has been derived and used in Figure 8a. While Betulaceae, Casuarinaceae, and Hamamelidaceae have correct grouping, the junction with Base divides *Nothofagus* from *Quercus*.

Group 6. Figure 9 differs from one already published by Martin and Dowd (1989); the two trees are of the same length but this one is preferred because it shows perfect pairing and reflects the order when only familial nodes are used. However, the other probably conforms better with taxonomy in that Dilleniaceae is separate from the other three families.

Group 7. Figure 10 shows that the two representatives of Juglandaceae pair leaving *Myrica*, the sole representative of Myricaceae, separate.

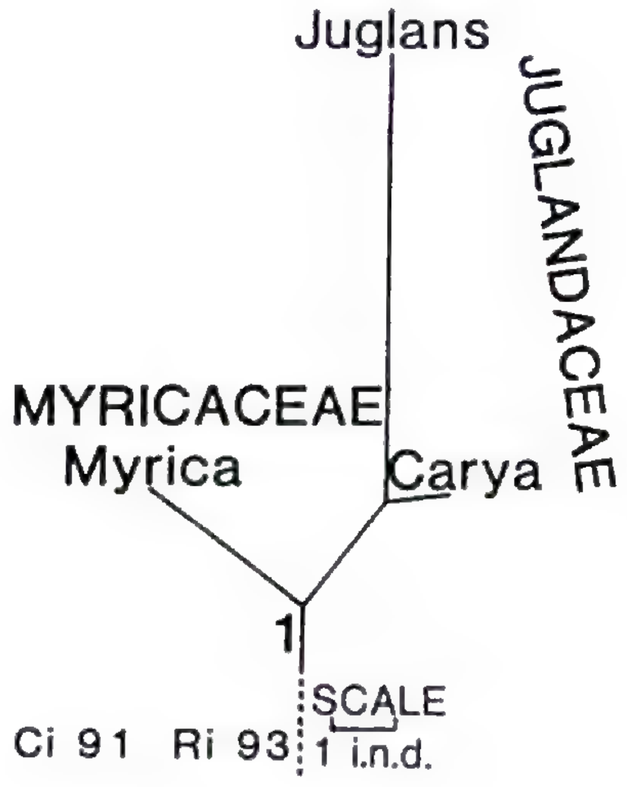


FIGURE 10. Group 7.

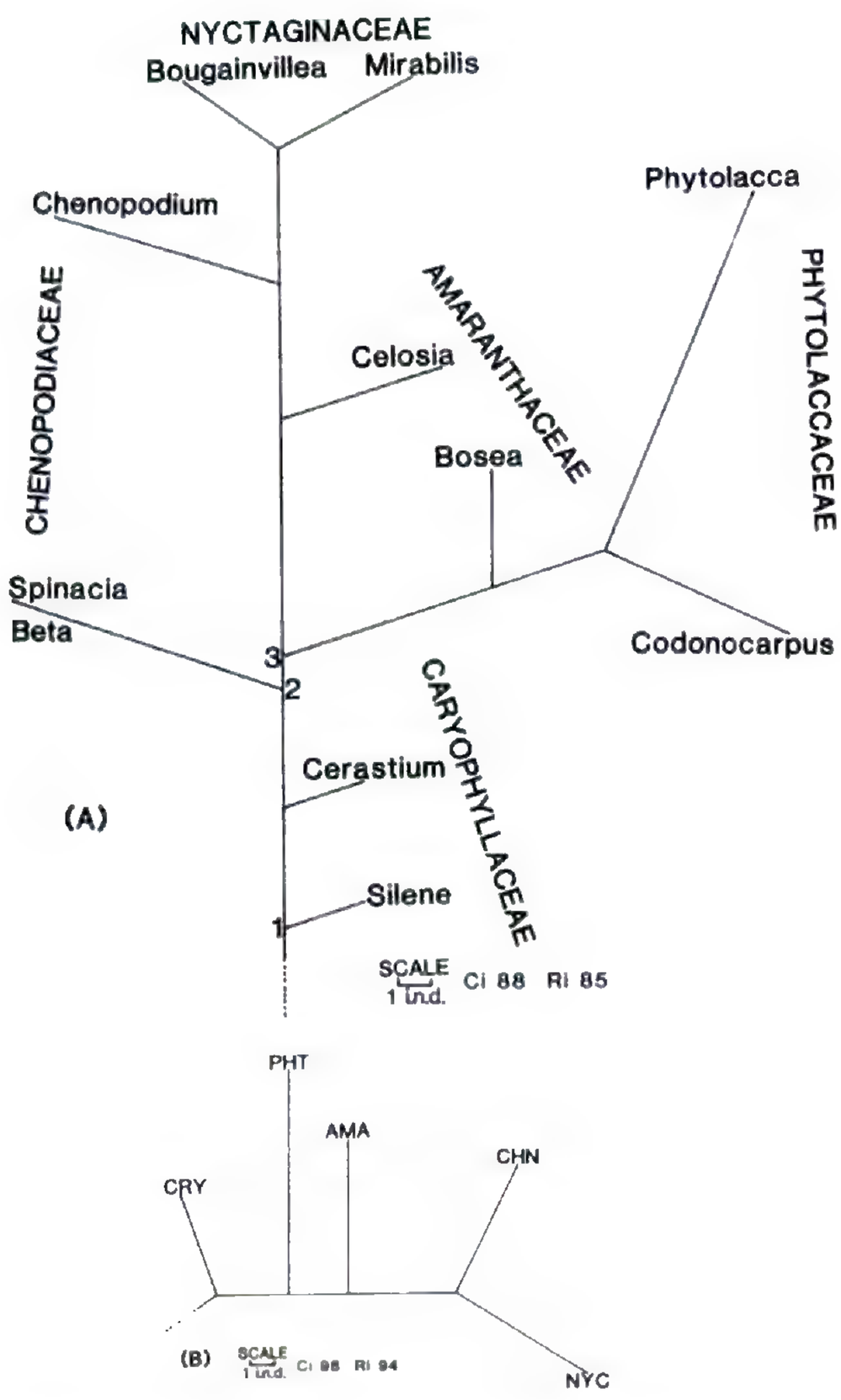


FIGURE 11.—(A). Group 8.—(B). Group 8 family nodes.

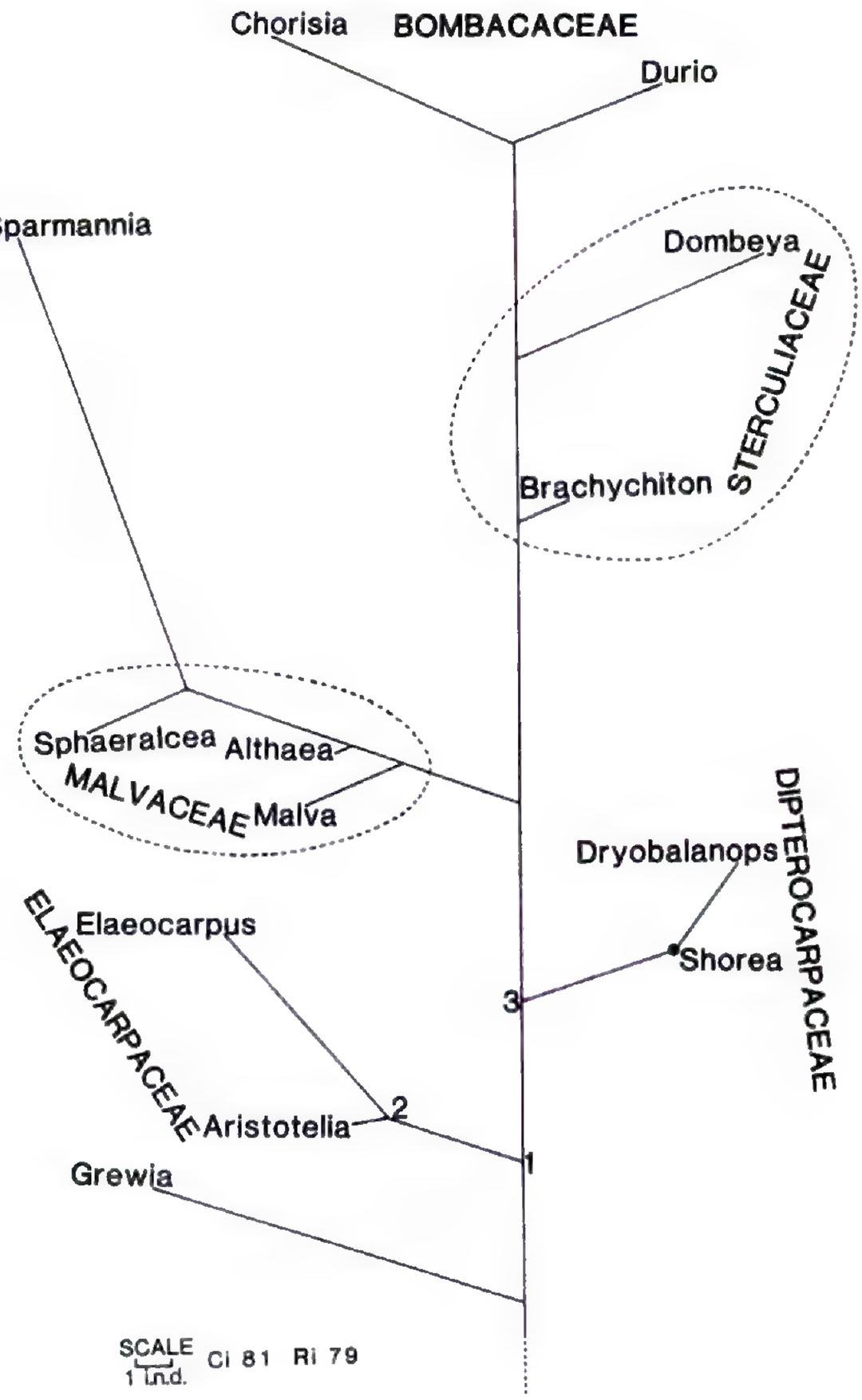


FIGURE 12. Group 9.

Group 8. The "Centrospermae" is one of the most unsatisfactory groups with representatives of two families, Chenopodiaceae and Amaranthaceae, failing to form pairs (Figure 11a). *Spinacia* and *Beta* have identical sequences, but these are quite different from *Chenopodium*. The tree for family nodes is in Figure 11b.

Group 9. There is a marked difference between the two representatives of Tiliaceae; *Grewia* is at the bottom of the tree (Fig. 12), while *Sparmannia* disrupts the clustering in Malvaceae. However, the remaining four families are satisfactory. *Grewia* was removed from Group 9 and added to the list of uncertain taxa. (As will be mentioned later, it subsequently rejoined.)

Group 10. While Violaceae, Cucurbitaceae, Salicaceae, Brassicaceae, and Flacourtiaceae formed good clusters (Fig. 13a), the two representatives of Datiscaceae (*Datisca* and *Tetrameles*) were very different. Attempts to study *Capparis* having failed, *Cleome* was left unpaired so we chose *Reseda* from the putatively related family Resedaceae. Since these two did group, we did not seek correct partners for them. In addition to these two singletons, *Moringa* represents a monogeneric family. A tree from family nodes is shown in Figure 13b.

Group 11. The representatives of all four families form pairs (Fig. 14), Myrsinaceae adjacently and the other three families dichotomously.

Group 12. As mentioned earlier, the two species of Epacridaeae are distinguished by having an additional amino acid inserted in their sequences. Although this could have been used as a character, it was unnecessary because the two species paired separately from the two Ericaceae species (Fig. 15).

Group 13. When family nodes are derived for Rosaceae, Cunoniaceae, and Saxifragaceae, they are very close (Fig. 16b), so it is not surprising that there is confusion when individual species are analyzed (Fig. 16a). The representatives of Rosaceae pair correctly, however.

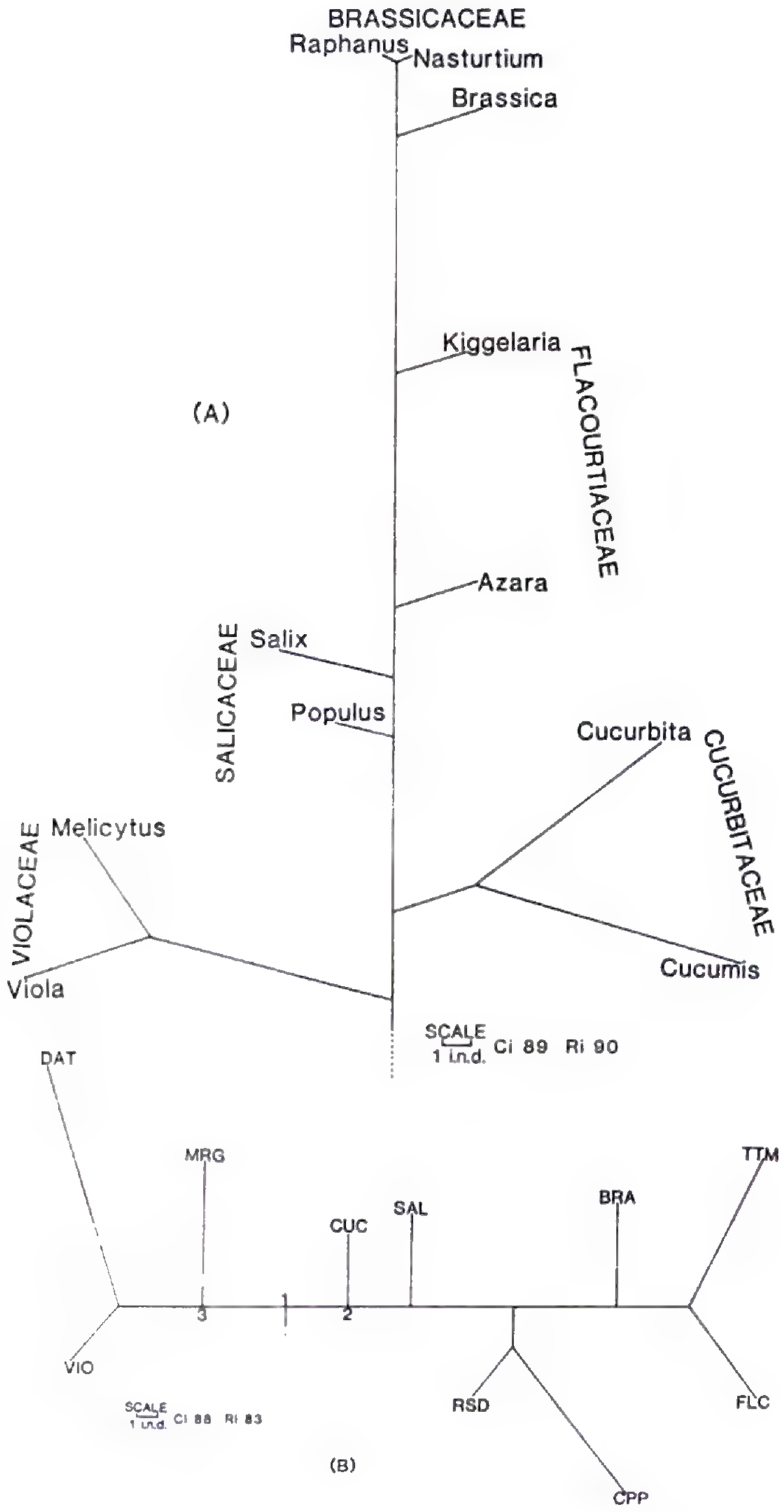


FIGURE 13.—(A). Group 10, omitting single representatives of families.—(B). Family nodes of Group 10. Because they did not pair and are sometimes placed in different families, *Datisca* and *Tetrameles* are included here.

Group 14. Among minimal trees derived when all legume species are analyzed simultaneously, there are some in which the two Mimosaceae species pair and so do the two Caesalpiniaceae; however, the eight Papilionaceae species are confused. We have therefore derived a Papilionaceae node separately (Fig. 17b) and show this with the other two families (Fig. 17a).

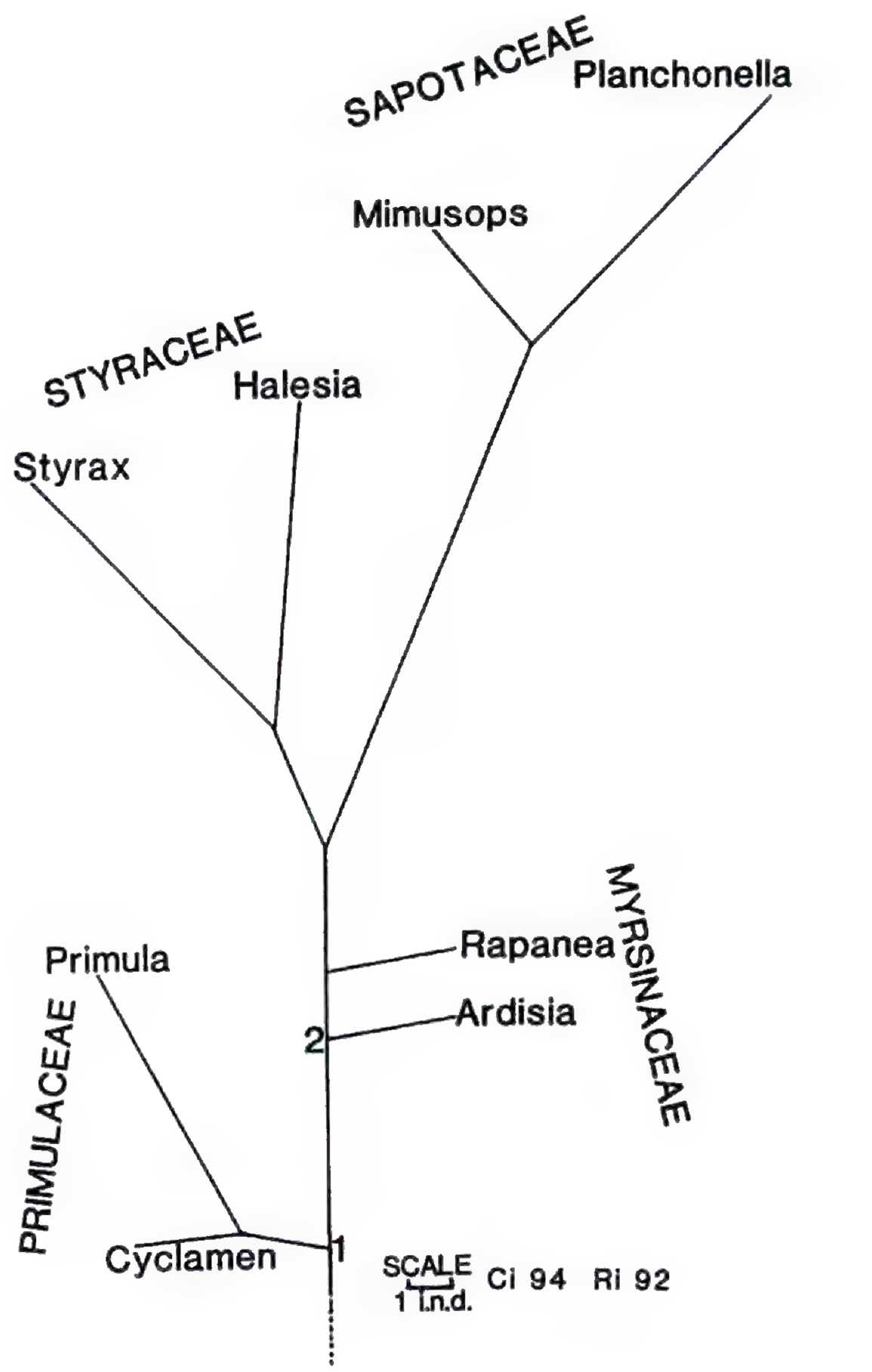


FIGURE 14. Group 11.

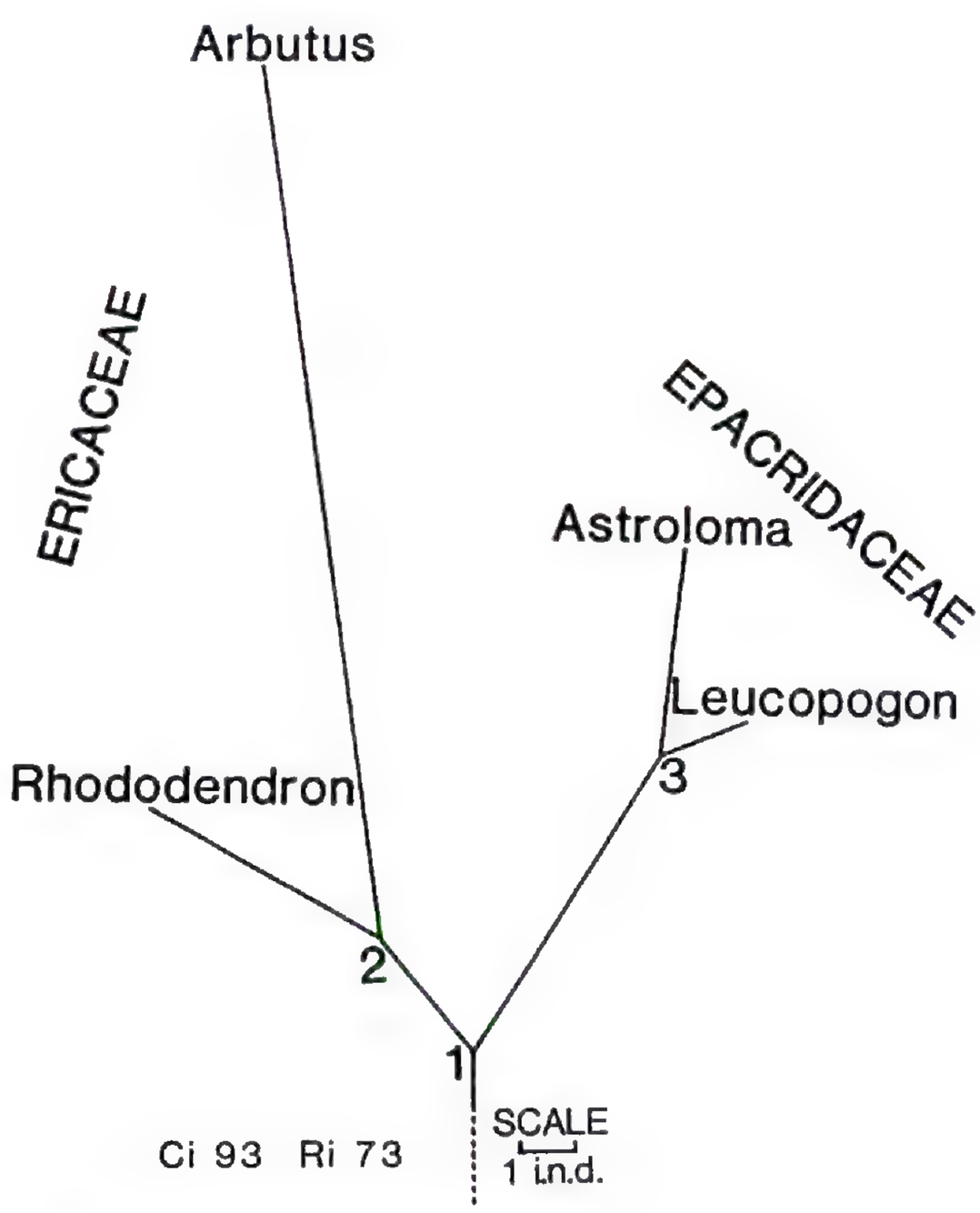


FIGURE 15. Group 12.

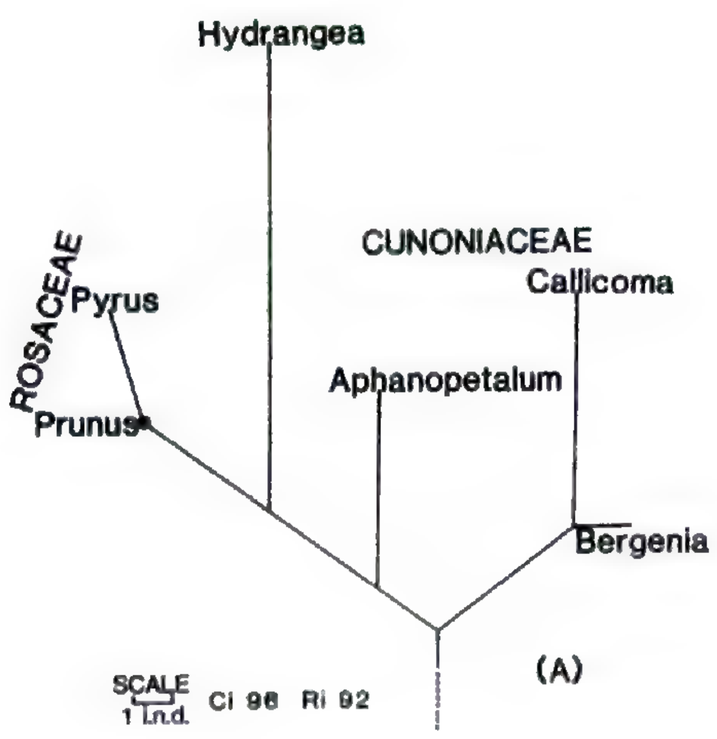


FIGURE 16.—(A) Group 13.—(B). Family nodes of Group 13.

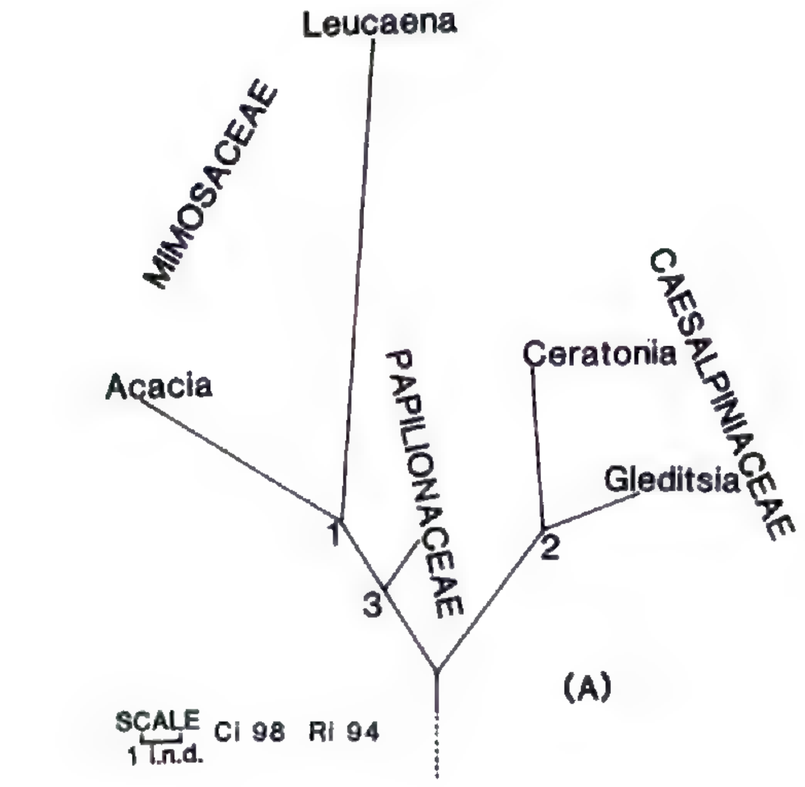


FIGURE 17. (A) Group 14 with Papilionaceae represented by a node derived from (B).

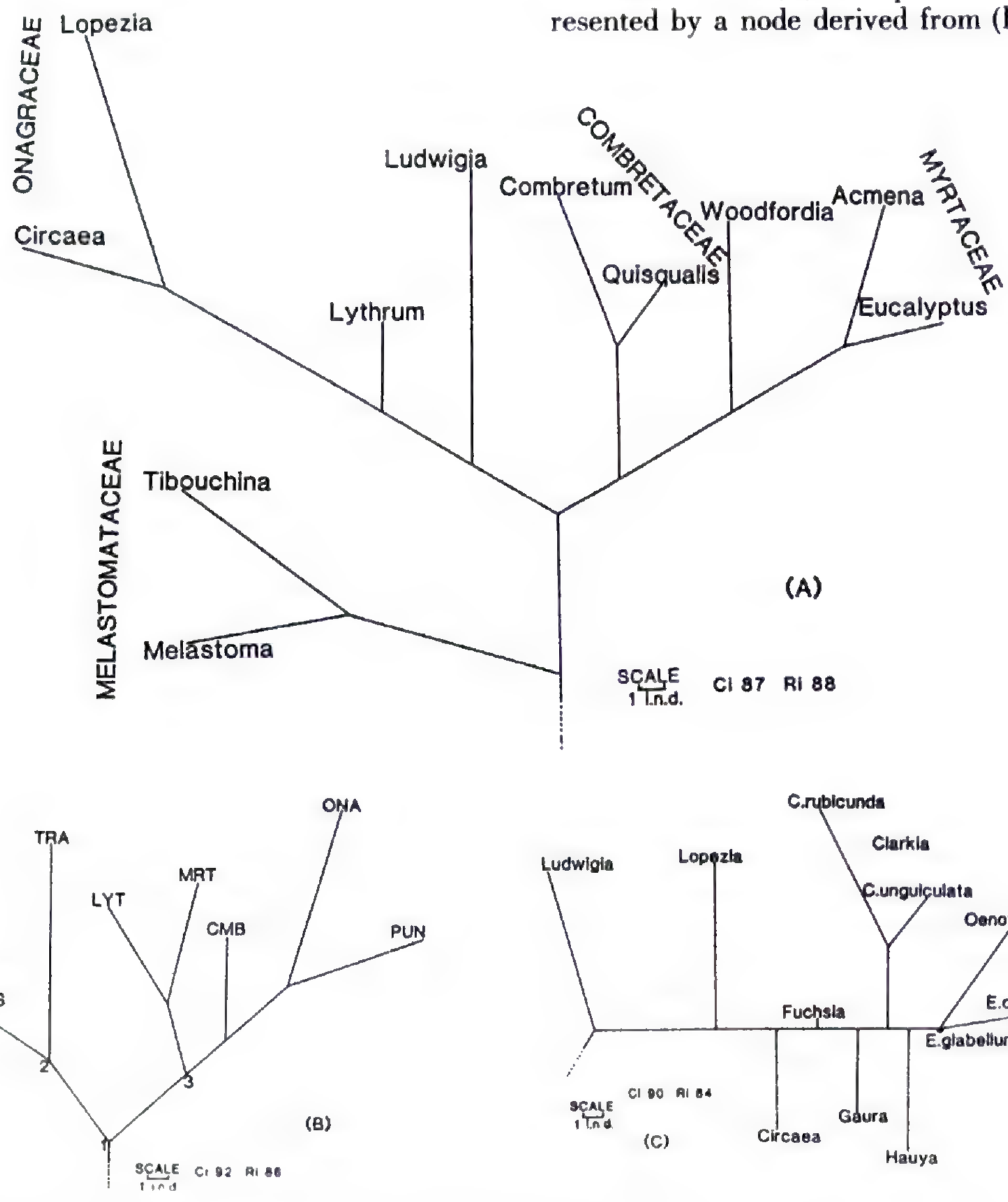


FIGURE 18. (A) Group 15 omitting *Trapa* and *Punica*, which are included with family nodes in (B). (C) Onagraceae.

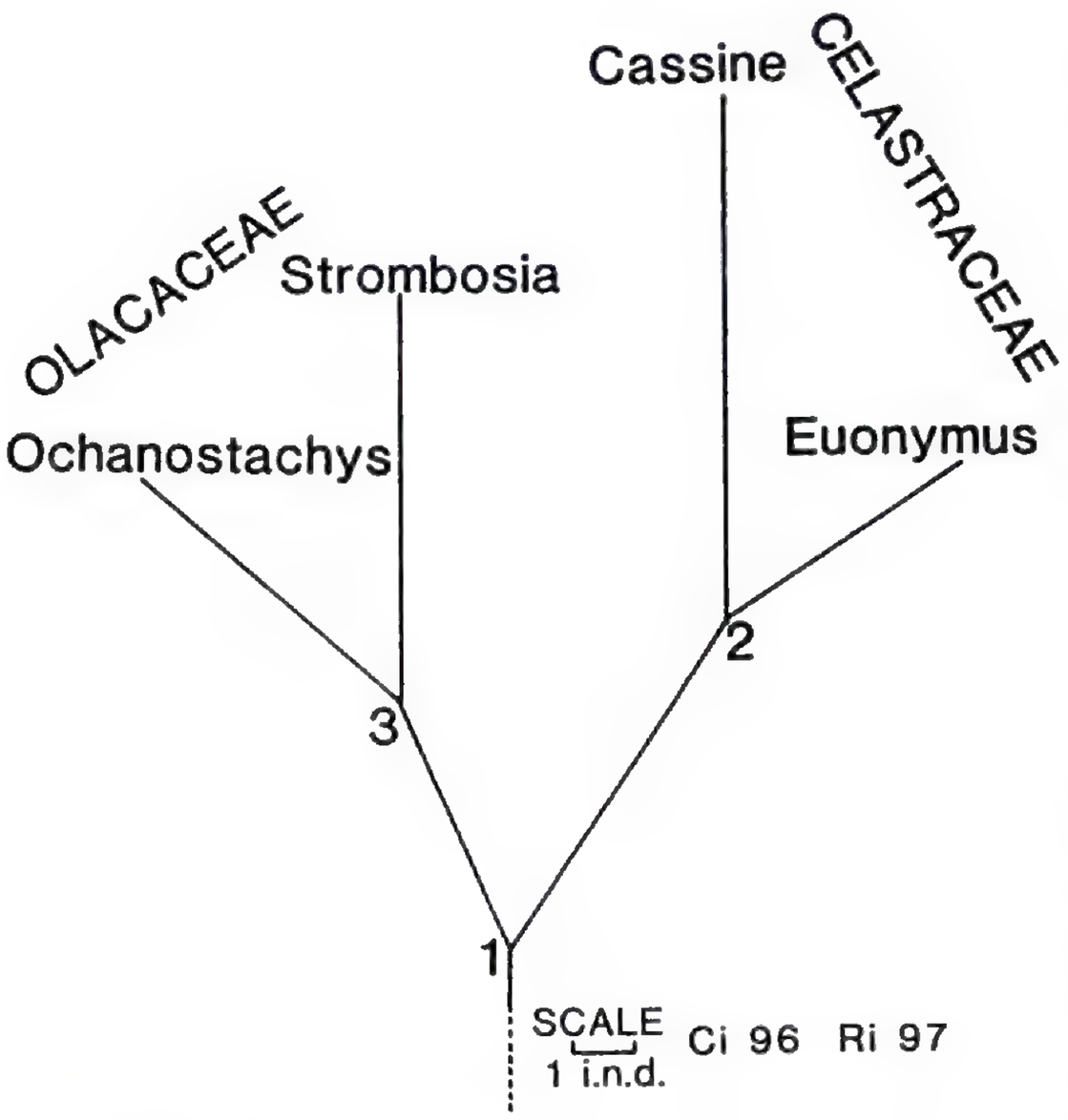


FIGURE 19. Group 16.

Group 15. This Group, which corresponds to the order Myrtales, was discussed by Martin and Dowd (1986a). Since then only *Trapa* and *Punica*, both singletons, have been added. When the representatives of the other five families are analyzed, pairing is good except in Lythraceae (Fig. 18a). The three members of Onagraceae in this tree are from the bottom of the family tree (Fig. 18c). When family nodes are analyzed (Fig. 18b), the root of the tree is in a different place from the one previously published; it is uncertain why this is so, but it could be due to the inclusion of new families, the earlier choice of inappropriate outgroups, or the new analytical methods.

Group 16. As discussed earlier, all representatives of the hemiparasites of the Santalales and Loranthaceae failed to yield protein samples, so this Group is reduced to Olacaceae and Celastraceae in which pairings are straightforward (Fig. 19).

Group 17. This Group is not very satisfactory possibly because, as indicated in Figure 20b, there has been a rapid radiation. The consequences are that the members of Simaroubaceae and Sapindaceae do not pair, while *Flindersia*, sometimes excluded from Rutaceae, does not group with the other two representatives of that family. However, there is good pairing for Connaraceae and Anacardiaceae (Fig. 20a). *Melia* having failed, *Cedrela* is left as the sole representative of Meliaceae.

Group 18. The two members of Haloragaceae, *Gonocarpus* and *Haloragodendron*, are so confounded with the three members of Rhizophoraceae (Fig. 21) that there was no point in deriving family nodes to derive a Group node.

Group 19. *Nitraria* having failed, *Zygophyllum* is a singleton as is *Tropaeolum*, for which no partner was available. As shown in Figure 22a, the members of Geraniaceae and Malpighiaceae pair. The family node tree is shown in Figure 22b.

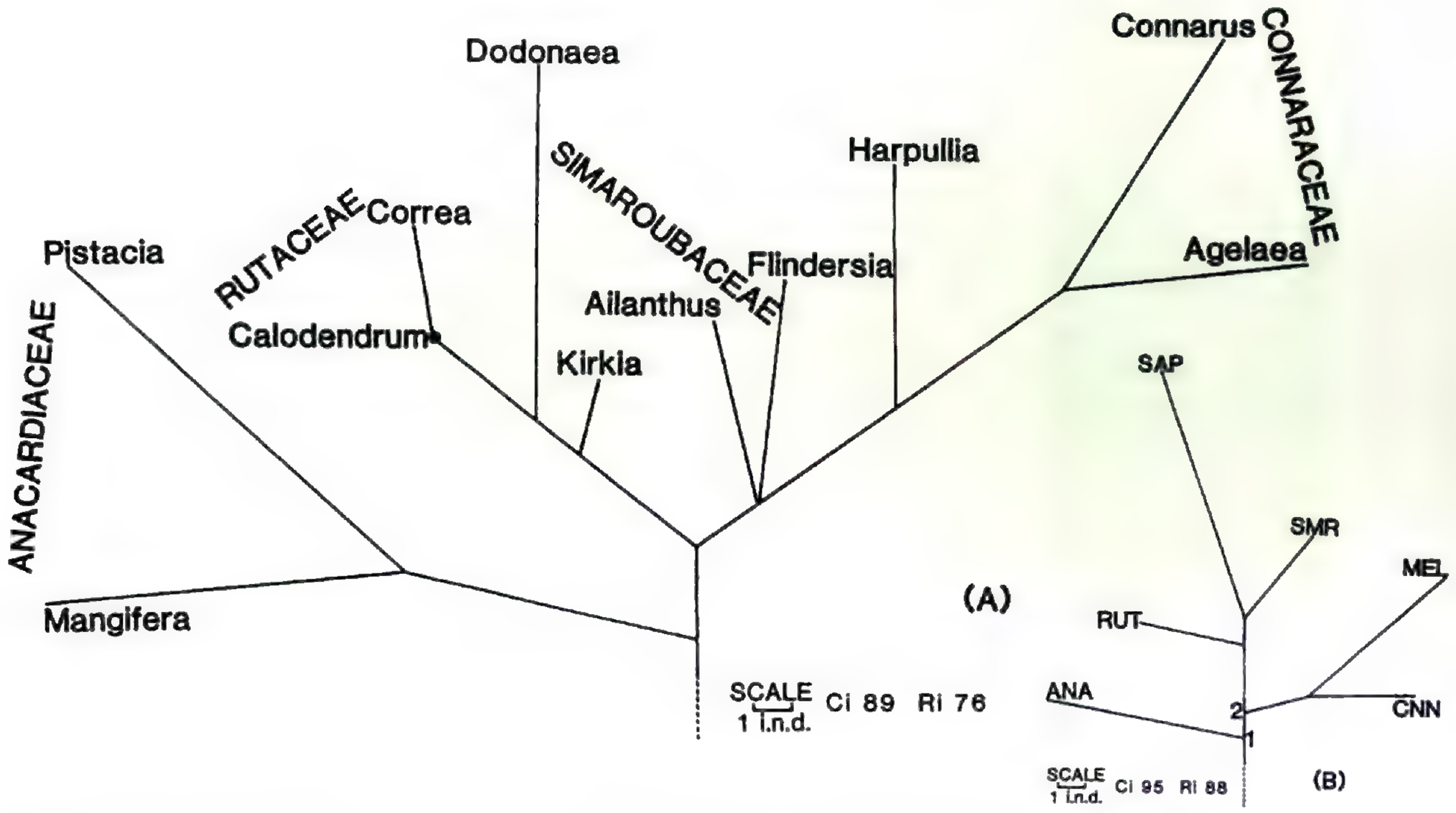


FIGURE 20. (A) Group 17 omitting *Melia*, which is included with family nodes in (B).

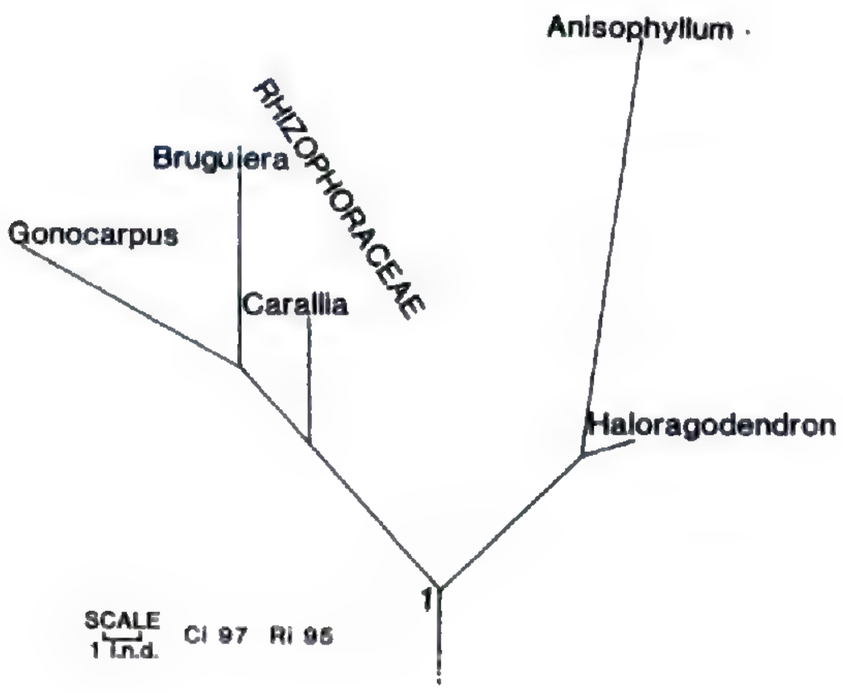
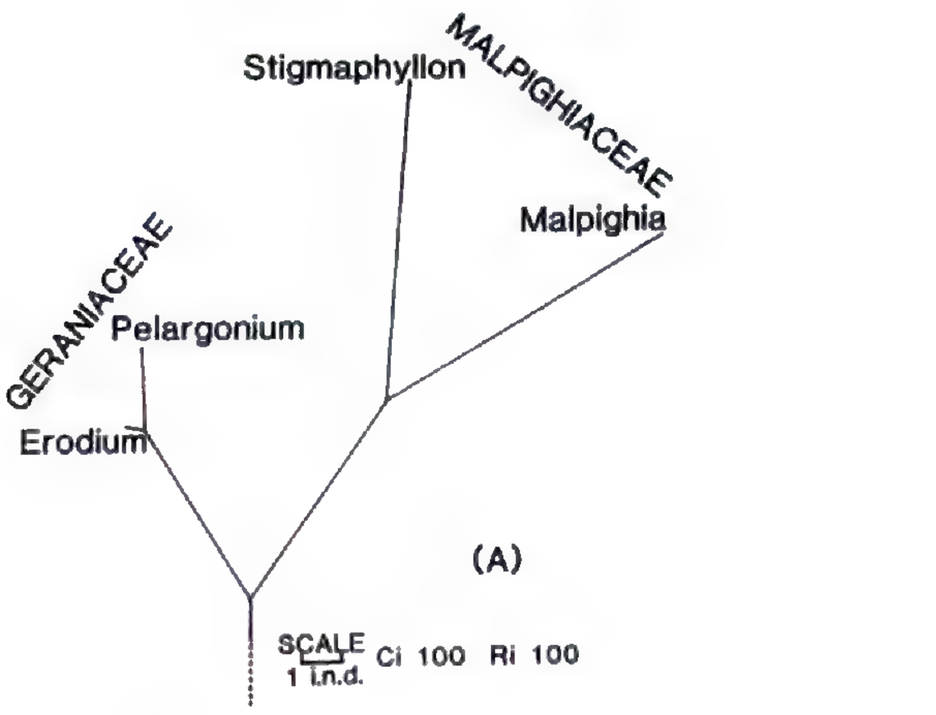


FIGURE 21. Group 18.

Group 20. *Hoya* was left a singleton by failure to extract protein from two other members of Asclepiadaceae, *Asclepias* and *Cryptostegia*. The members of four families showed dichotomous pairing while *Logania* paired alongside *Buddleia*, which is only possibly a member of Loganiaceae (Fig. 23).

Group 21. The representatives of Lamiaceae and Verbenaceae were very similar but there was nevertheless a minimal tree in which congruent pairing occurred (Fig. 24).



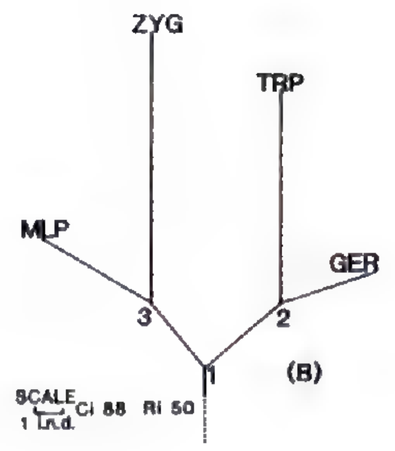


FIGURE 22. (A) Group 19 omitting *Zygophyllum* and *Tropaeolum*, which are included in (B).

Group 22. There have been previous reports of *Solanum* (Martin et al., 1986) and *Nicotiana* (Martin & Dowd, 1984b). Using HENNIG86, new

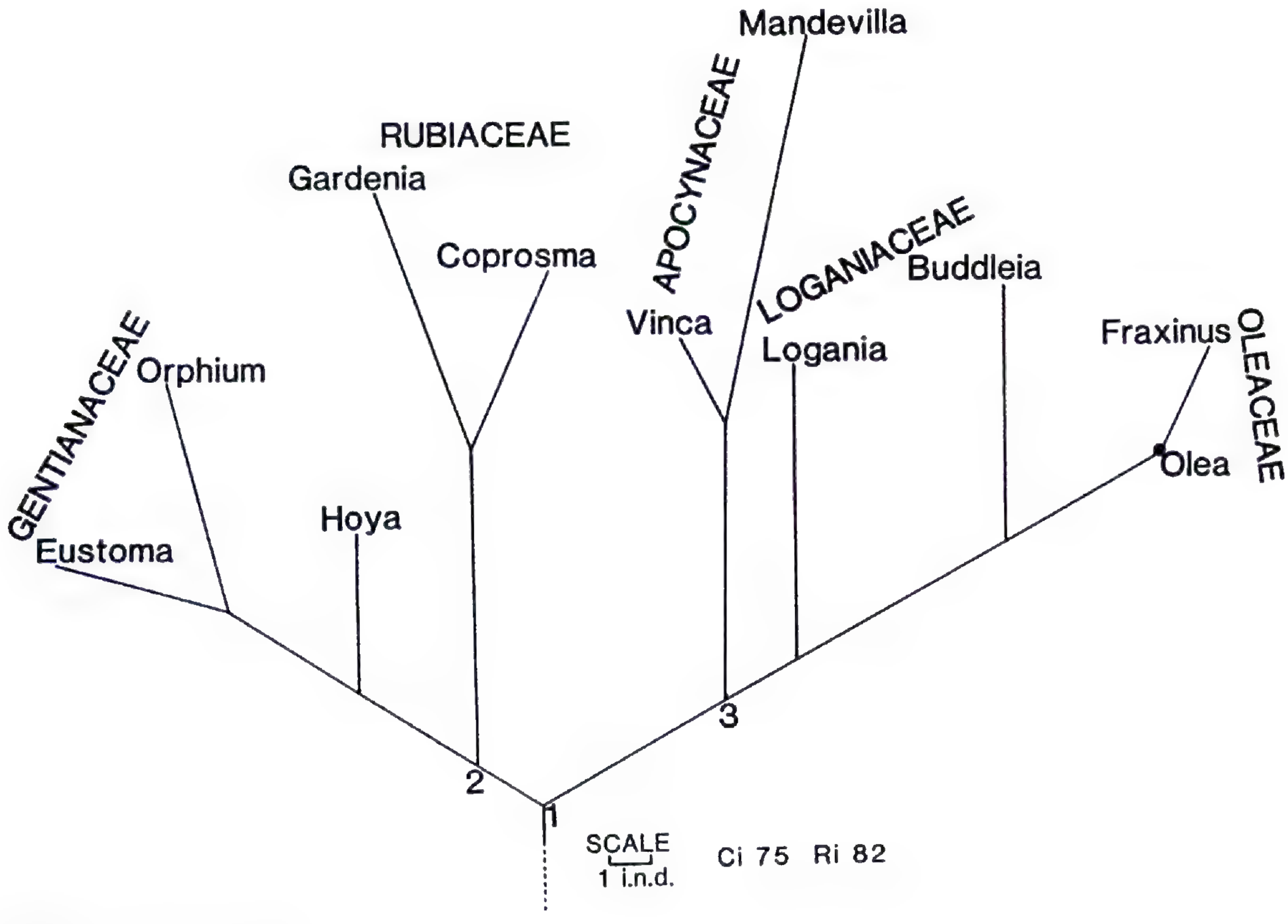


FIGURE 23. Group 20.

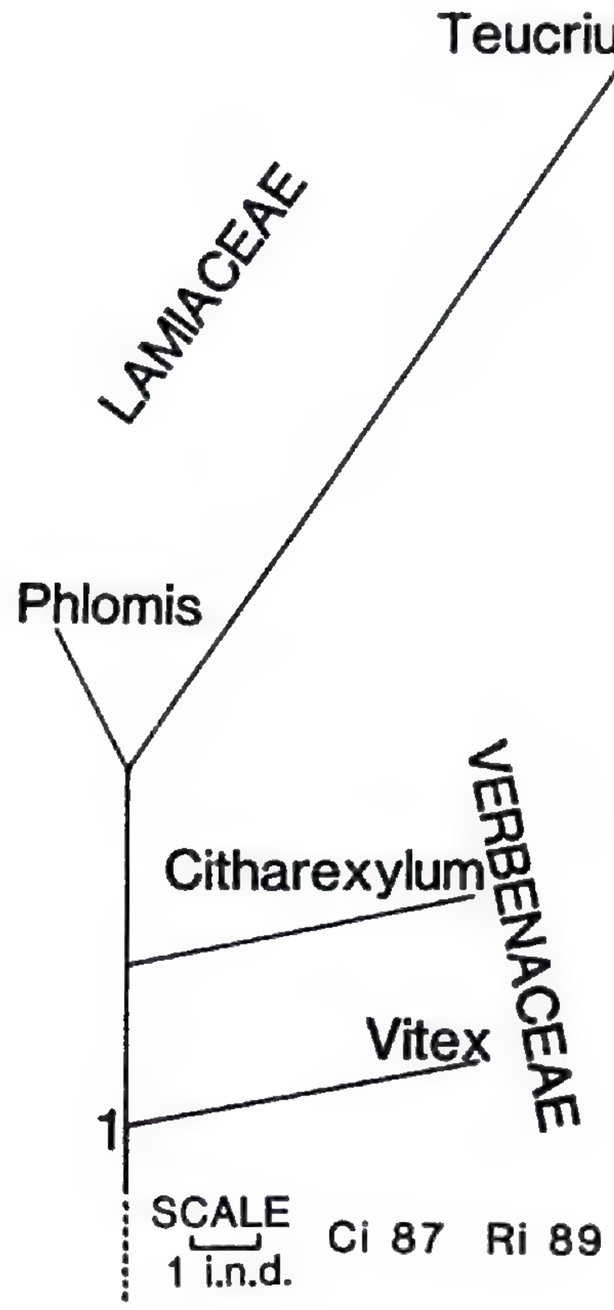


FIGURE 24. Group 21.

nodes have been derived for both genera (Fig. 25b, c) and were used, with *Anthocercis*, to represent Solanaceae in Figure 25a. These group well but there is confusion between the representatives of Convolvulaceae and Polemoniaceae.

Group 23. As mentioned earlier, all attempts to extract rubisco from Acanthaceae species failed. The representatives of the other four families of this Group pair well, Scrophulariaceae, Gesneriaceae, and Bignoniaceae dichotomously and Pedaliaceae adjacently (Fig. 26).

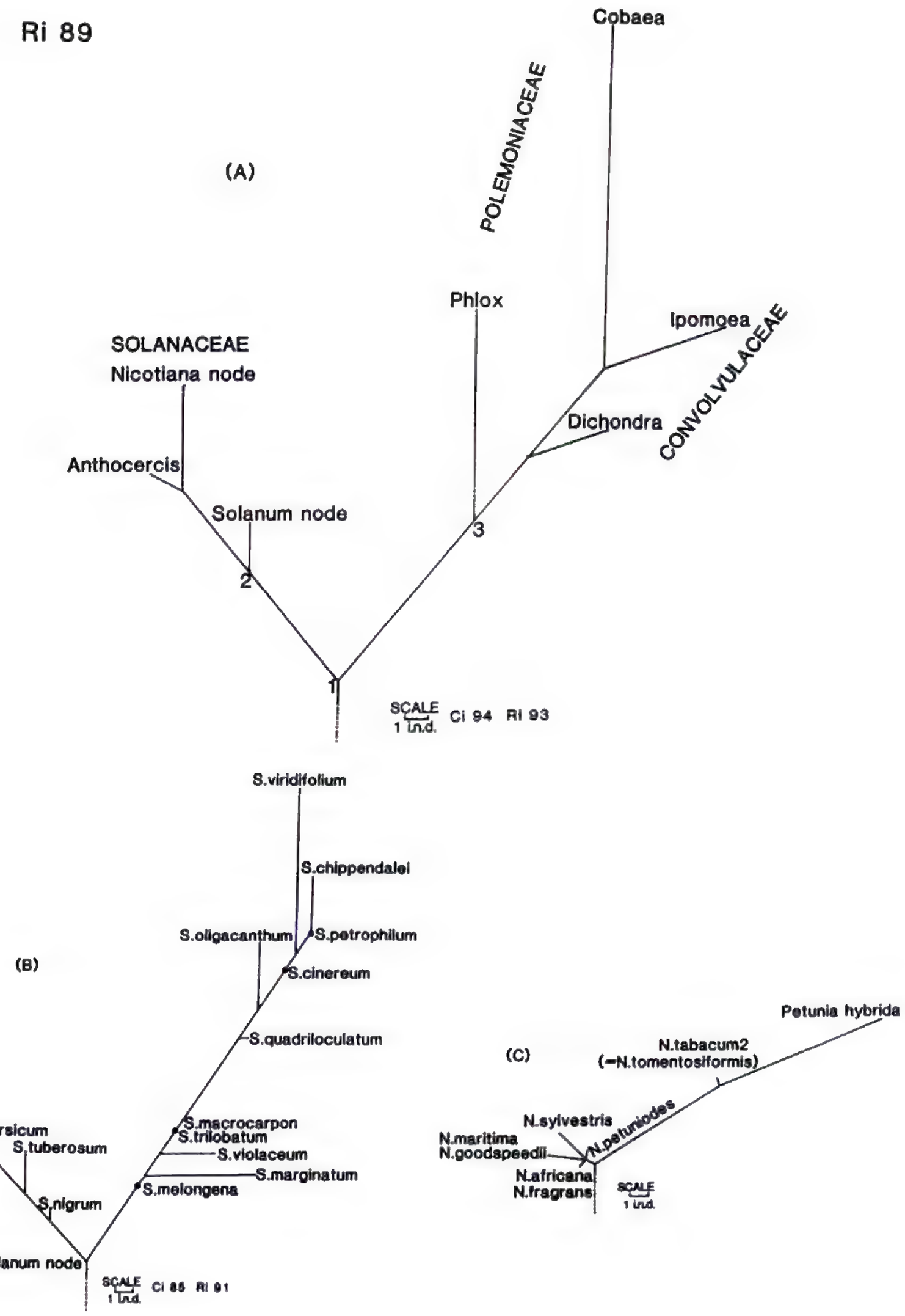


FIGURE 25. (A) Group 22 with the *Solanum* node derived from (B) and the *Nicotiana* node from (C).

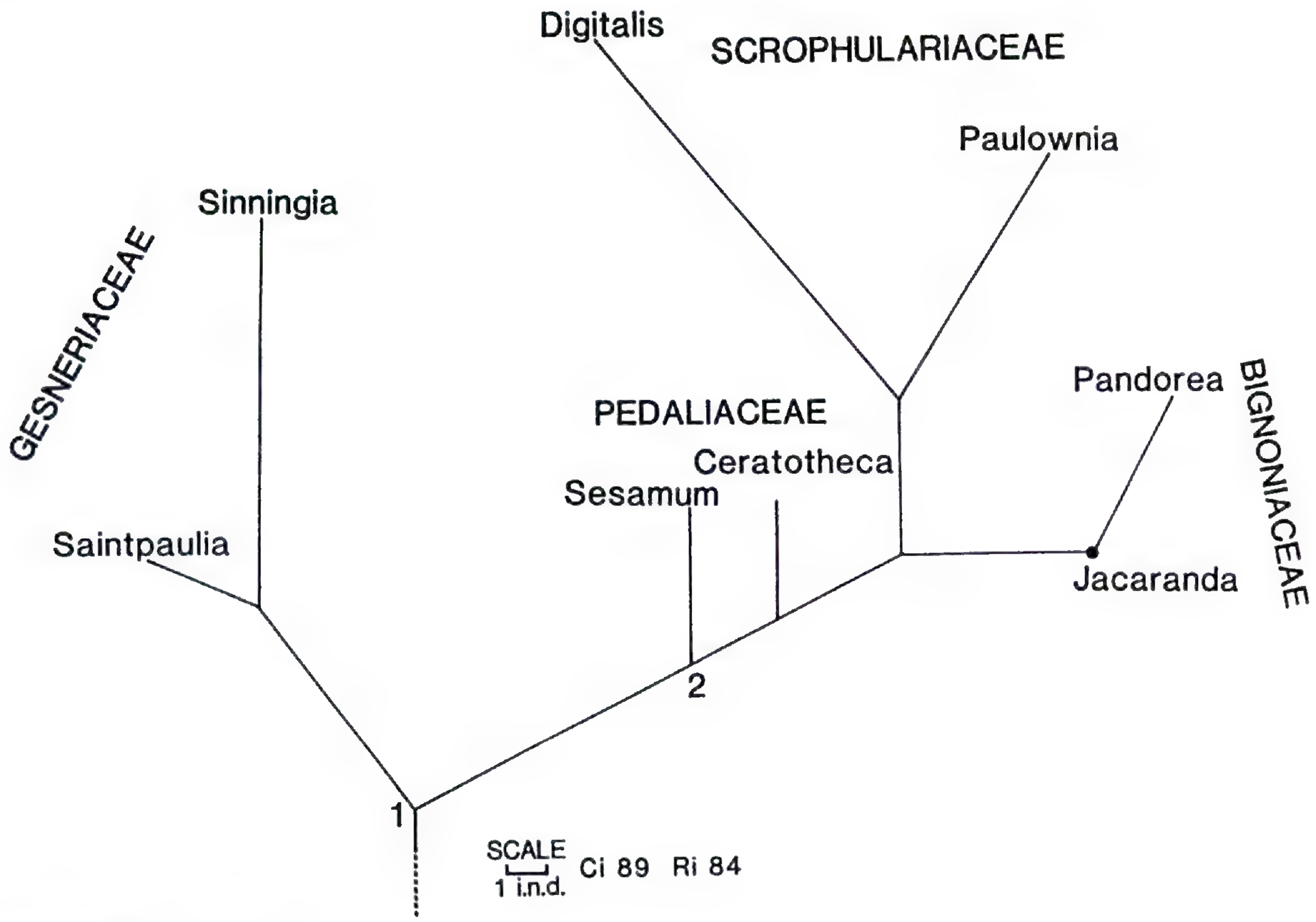


FIGURE 26. Group 23.

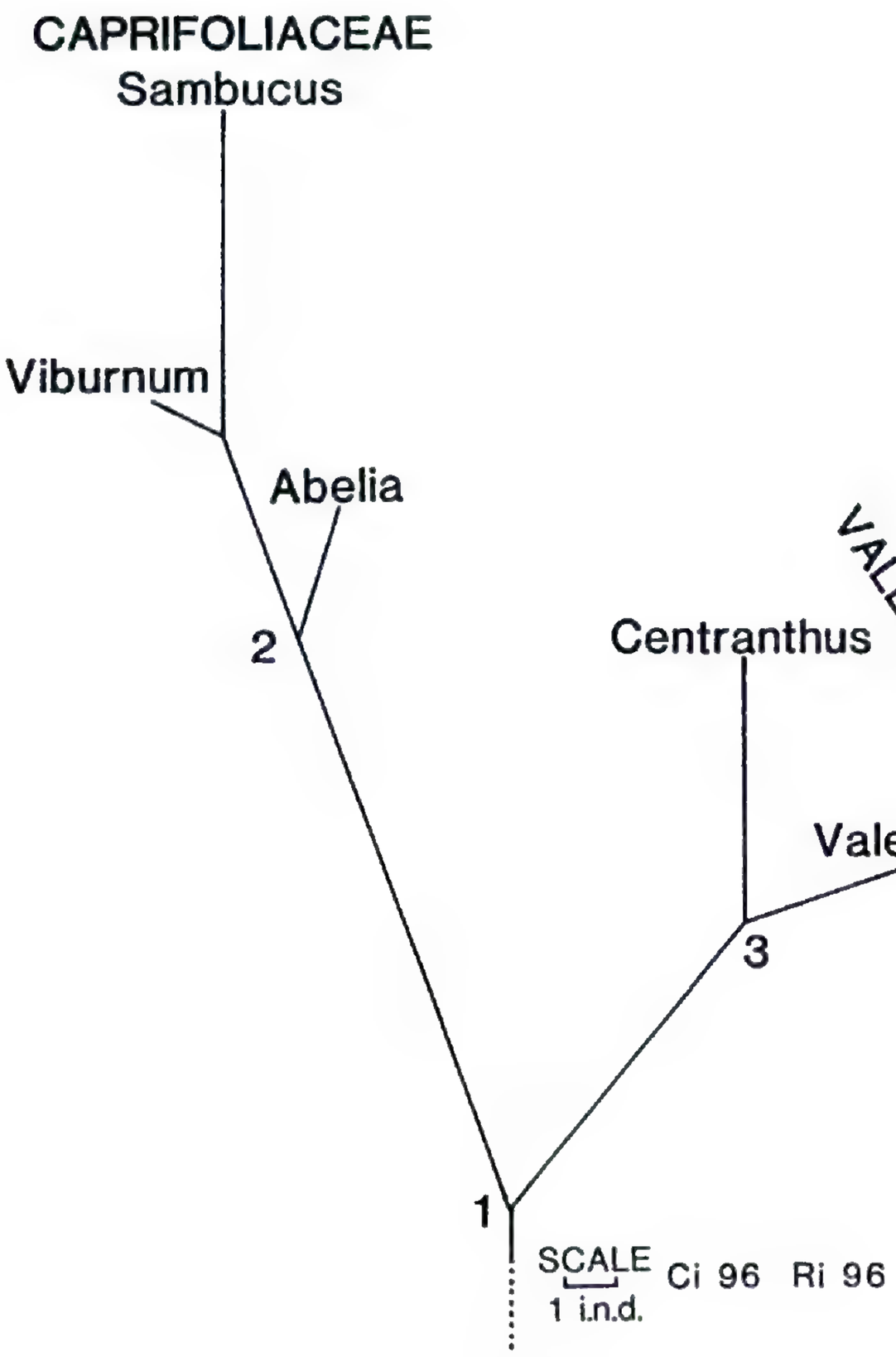


FIGURE 27. Group 24.

Group 24. The three members of Caprifoliaceae are substantially different from the two members of Valerianaceae so that correct grouping is observed (Fig. 27).

Group 25. This Group is unusual in that *Apium* and *Foeniculum* of Apiaceae have identical sequences as do *Schefflera* and *Fatsia* of Araliaceae. Consequently, the tree of this Group (Fig. 28) is very simple.

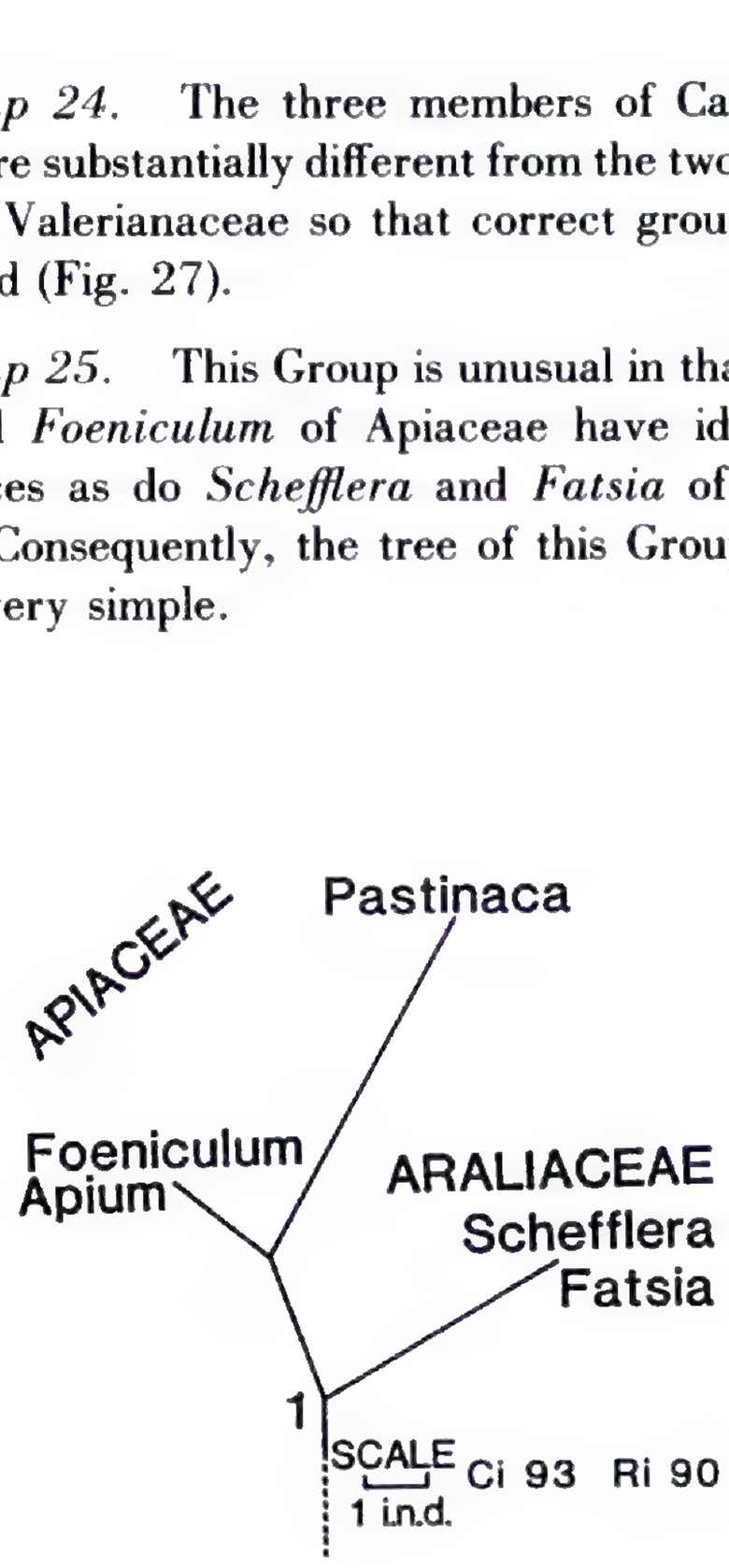


FIGURE 28. Group 25.

The Derivation of a Tree for the Groups of Dicotyledons

first stage; a test of the reality of groups

Depending on the size and complexity of the Group, one, two, or three nodes have been marked near the bases of each Group tree; altogether there are 58 basal nodes and the ancestral sequence of each has been derived using ANALYZE. These have been used for a test of the reality or integrity of the Groups. If a family does not really belong to a Group, it should usually behave like an outgroup and assume the position closest to the base of the tree. Thus, in a simultaneous analysis of all 58 basal nodes, it would be expected that nodes truly belonging to the same Group should cluster together. If a family is misplaced in a Group, the nodes should separate.

The only program that can be used with 58 taxa simultaneously is HENNIG86 with the option *mhennig* followed by *bb*. This was done three times, each yielding large numbers of trees for which strict consensus trees were derived. Inspection indicated that most Groups behaved as if they were real, but some separation of nodes occurred in Groups 5, 8, 14, 15, 22, and 24 (see below). It is unlikely that this sort of analysis would give a completely reliable result, but our interpretation is that where there is no separation of within-Group nodes, that Group should be accepted as valid. We understand that our test is not infallible, but we are reluctant, at this stage, to attempt another obvious test, viz. the simultaneous analysis of adjoining Groups. This test was used earlier with Groups 1, 2, and 3 and led to considerable mixing of the first two. The amount of convergent evolution between Groups is probably such that, if this test were applied widely, confusion would result. Therefore, even though we understand the limitations, we confine our testing of the integrity of Groups to one sort of analysis.

For the six Groups where there was doubt, we applied the test devised by Lake (1987). This is confined to four species, A, B, C, D and uses a chi-square test to decide which is the most probable of the three possible relationships, viz. A + B & C + D or A + C & B + D or A + D & B + C. Thus representatives of each part of a divided Group were tested with representatives of the Groups with which they most closely clustered. These tests gave no further grounds for doubting the integrity of Groups 8 and 15 and consequently, in the next stage of the analysis, they were included unchanged. The tests reinforced the doubts about Groups 14, 22, and 24, so their separate parts were added to the list of uncertain families to be incorporated later. These were: from Group 14, Mimosaceae plus Papilionaceae on the one hand and Caesalpiniaceae on the other; from Group 22, Convolvulaceae plus Polemoniaceae on the one hand and Solanaceae on the other; from Group 24, Valerianaceae and Caprifoliaceae. Tests with Group 5 were equivocal, so Hamamelidaceae was removed and added to the list of uncertain families, but the node for the remaining three families was used at the next stage.

second stage; deriving a preliminary, abbreviated tree

Following the first stage, the basal node was used to represent each of the 22 remaining Groups (though amended in Group 5 after removal of Hamamelidaceae). Several analyses, using *mhennig* and *bb*, were carried out on these nodes. The object was to identify apparently constant associations from which nodes might be derived in order to reduce the number of taxa to 16, a number compatible with analyses using the reliable *ie* program at the next stage. The following five pairings were chosen and their nodes derived: Groups 2 and 3; Groups 6 and 16; Groups 7 and 9; Groups 11 and 19; Groups 21 and 23. Group 25 was omitted at this stage because it was small, well-defined by morphology and our own work and could be incorporated later in the same way as the uncertain taxa. The resulting tree of 16 taxa is shown in Figure 29.

third stage; incorporating taxa of uncertain affinities

At this point there were 28 taxa on the list of those with uncertain affinities, comprising 18 families that were not placed in a Group (see Table 1 but note that Piperaceae and Nelumbonaceae were considered earlier), two genera (*Humulus* and *Grewia*) excluded from Groups during their analysis, five families and two pairs of families excluded during the first stage, and Group 25 omitted at the second stage. We wanted to add these into the second stage tree as accurately as possible using the *ie* program. These analyses with 17 taxa could each be performed in about a day. Although there was some variation, the second stage tree remained reasonably stable during these analyses, and we noted where each uncertain taxon fit. Six joined

in the basal third, 14 in the middle third, and 16 in the distal third. (The nonadditivity reflects that rigid demarcation was not exercised and borderline taxa were placed in two sets.) The members of each of the three sets were then analyzed with the corresponding members of the second stage tree and possible new or amended Groups were identified.

FOURTH STAGE; REDEFINITION OF GROUPS

Putative new or amended Groups were tested extensively to ensure that they were real. In this process an important factor in determining the coherence of Groups was the length of the internode joining a hitherto uncertain member to the Group. Penny et al. (1987) have emphasized that "long edges attract," and we have long been aware that the junction of a distantly connected taxon is subject to so much variation that it is scarcely reliable. Thus, we have usually rejected a potential new member of a Group if it joins with a disproportionately long internode and have left it as uncertain.

In three cases, definite hypotheses arising from our work could be tested. In each case the question was whether a taxon belonged to the Group to which it was initially assigned (Table 1) or to the Group indicated by stage 3. This could be answered by considering the lengths of the alternative trees. In two cases, *Humulus* and Hamamelidaceae, the new grouping was shorter and therefore preferred. For *Grewia*, the trees were the same length so there was no good reason for preferring the new grouping (with Group 18).

As a consequence of these tests, only 15 of the original 25 Groups have the same composition as they had before the first stage of this section. The other ten Groups have been increased, decreased, or merged. Where a nucleus of an original Group remains, the number has been retained but A added. Original Groups 13, 24, and 25 have disappeared. New Groups 26, 27, 28, and 29 have been formed.

Group 4A. *Humulus* has been removed.

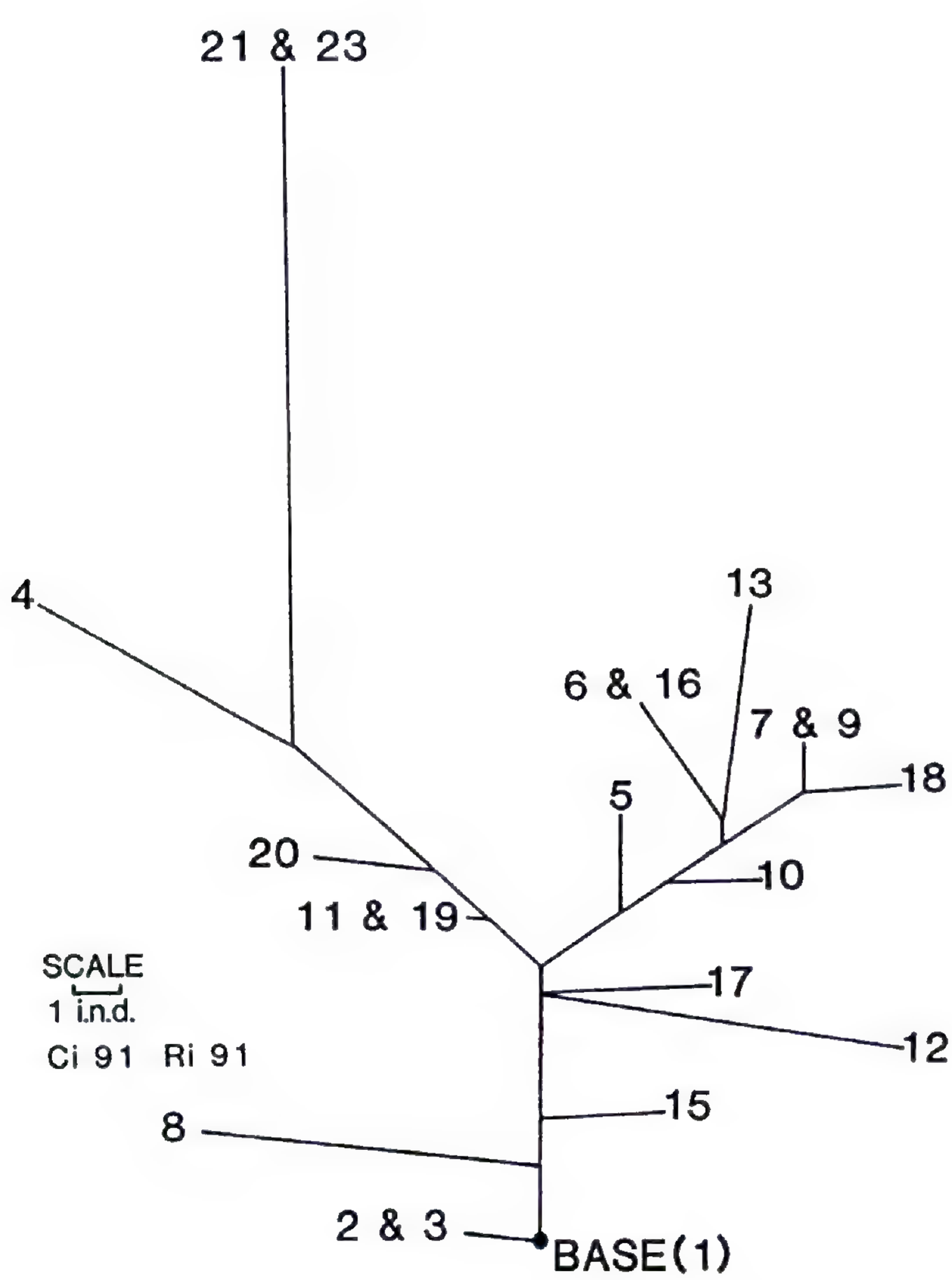


FIGURE 29. The provisional tree of Group nodes abbreviated by combining some Groups and omitting others that had dissolved.

Group 5A. Hamamelidaceae has been removed.

Group 8A. Although the original Group 8 ("Centrospermae") remains intact, Lecithydaceae and *Humulus* join the same branch of the tree (Fig. 30).

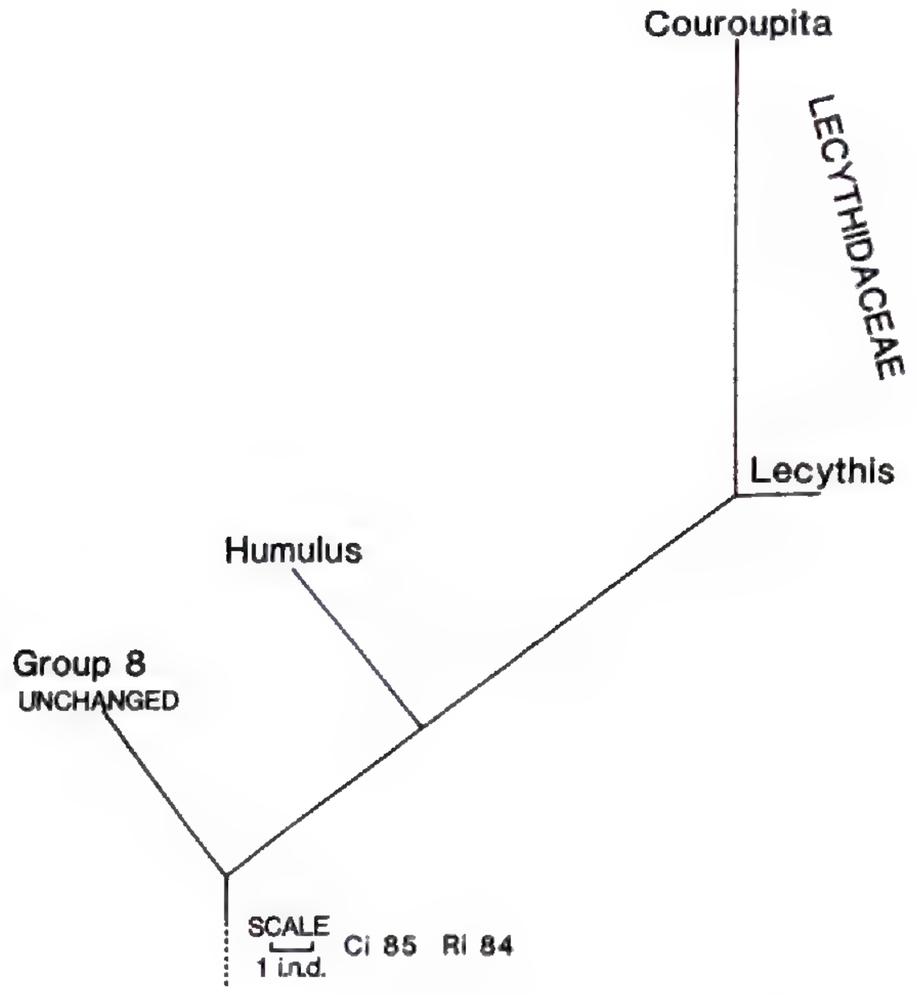


FIGURE 30. Group 8A. See Figure 11 for Group 8.

Group 12A. At all stages, Convolvulaceae and Polemoniaceae grouped separately from Solanaceae, the other member of Group 22. At the third stage, along with Polygonaceae, they clustered with Group 12 (Fig. 31). Polemoniaceae and Ericaceae are confused, but the other three families grouped appropriately.

Group 14A. The second stage tests suggested that the legumes should be divided between Caesalpiniaceae on the one hand and Mimosaceae and Papilionaceae on the other; Caesalpiniaceae clustered with Group 13. A series of Lake tests (see "First stage" above and Martin & Dowd, 1990) was therefore performed. These tests strongly indicated, first, that Caesalpiniaceae was closer to Rosaceae than to either of the other two legume families and, second, that Mimosaceae and Papilionaceae were closer to other Groups (e.g., Connaraceae in Group 17, Chrysobalanaceae in Group 18A below) than were Caesalpiniaceae and Rosaceae.

Other second stage tests had indicated that Proteaceae, *Coriaria*, *Crossosoma*, and Hamamelidaceae were also linked to the complex of Groups 13 and 14. The tree that resulted when these were

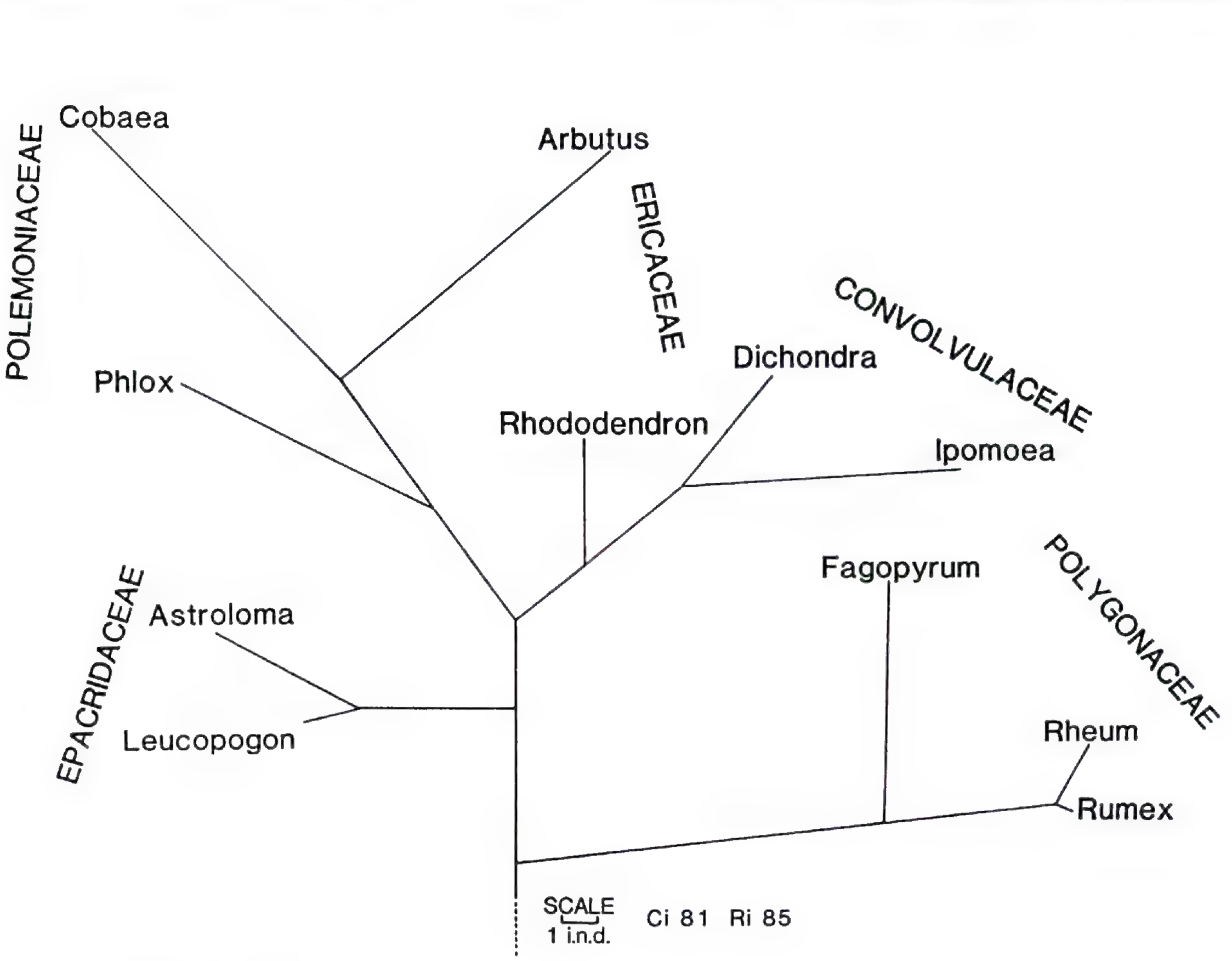


FIGURE 31. Group 12A.

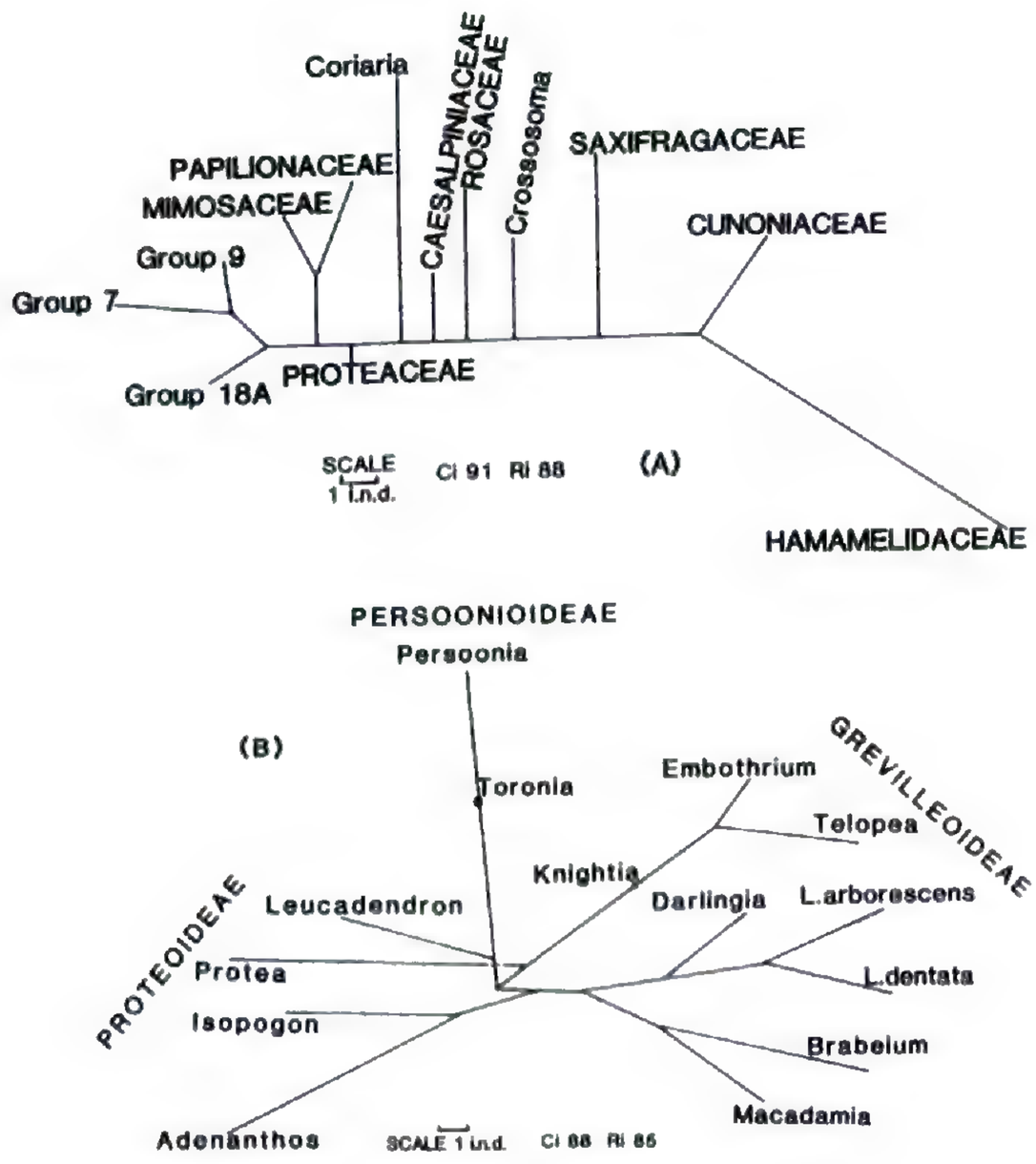


FIGURE 32. (A) Group 14A. For three legume families see Figure 17, and for Proteaceae see (B).

all analyzed together is shown in Figure 32a. The Proteaceae node was derived from Figure 32b, while the Mimosaceae–Papilionaceae node is node 3 of Figure 17a.

Group 18A. Third stage tests suggested that the Chrysobalanaceae and Vitaceae might cluster with Group 18 and also with Group 25 (Apiaceae and Araliaceae). Incorporation of these (Fig. 33) does nothing to repair the previous (Fig. 21) disjunction of Haloragaceae while Rhizophoraceae s.l. remain apart from Anisophyllea.

Group 22A. With the other two families joining Group 12A (above), the Solanaceae were left as the sole representative.

Group 26. This new Group (Fig. 34a) consists of three families (Campanulaceae, Caprifoliaceae and Goodeniaceae), each with well-paired representatives. With them is Asteraceae, the node for which is derived from Figure 34b.

Group 27. This comprises the families Elaeagnaceae and Rhamnaceae, the members of which form pairs (Fig. 35).

Group 28. As noted below, *Buxus* does not pair with *Simmondsia*, which is sometimes placed in Buxaceae. While the latter clusters with Euphorbiaceae (Fig. 36), *Buxus* does not.

Group 29. The species of Hydrophyllaceae, Thymelaeaceae, and Valerianaceae form pairs in this new Group (Fig. 37).

TAXA THAT REMAIN UNPLACED

There are three families for which we have no acceptable hypothesis. (a) *Loasaceae.* It was un-

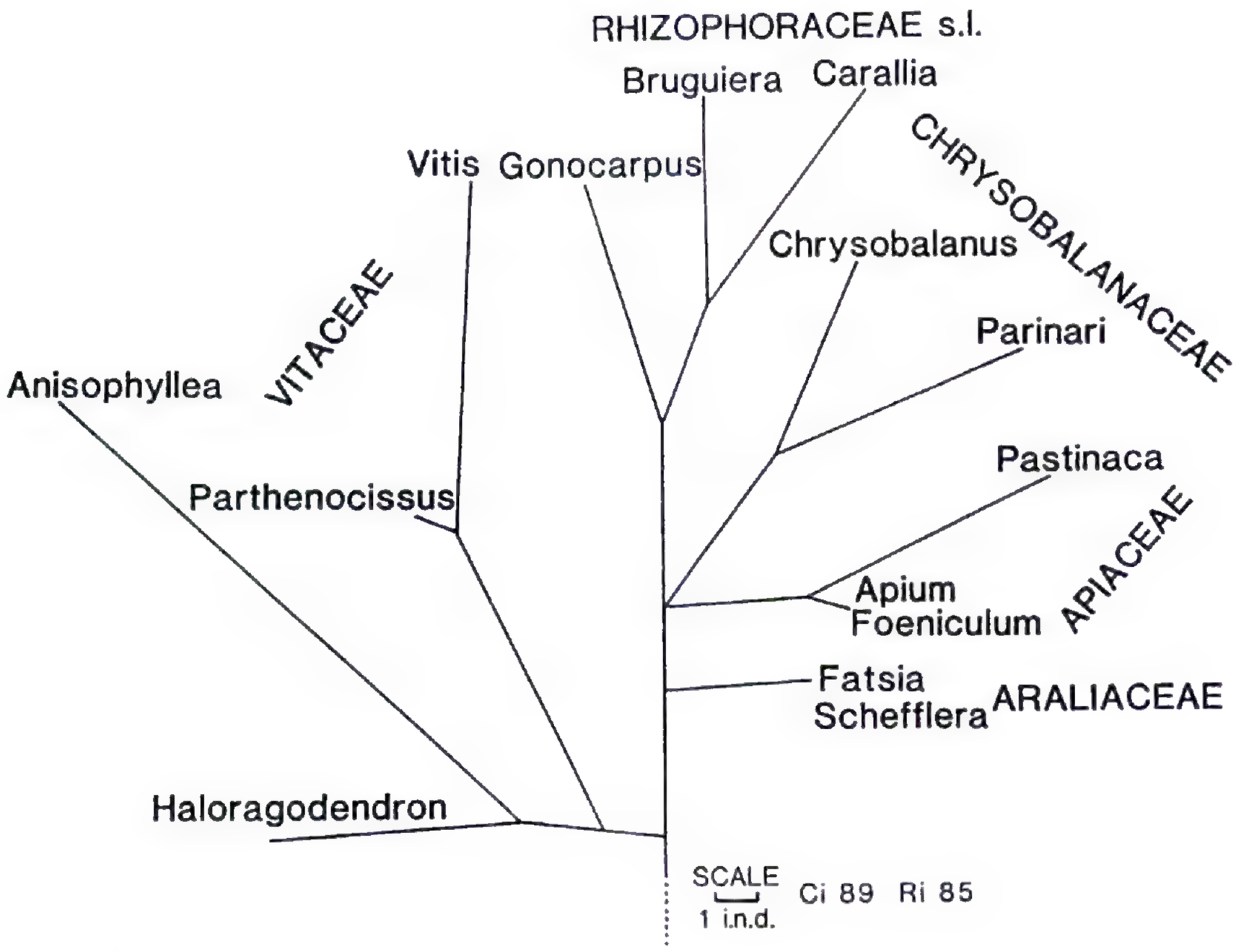


FIGURE 33. Group 18A.

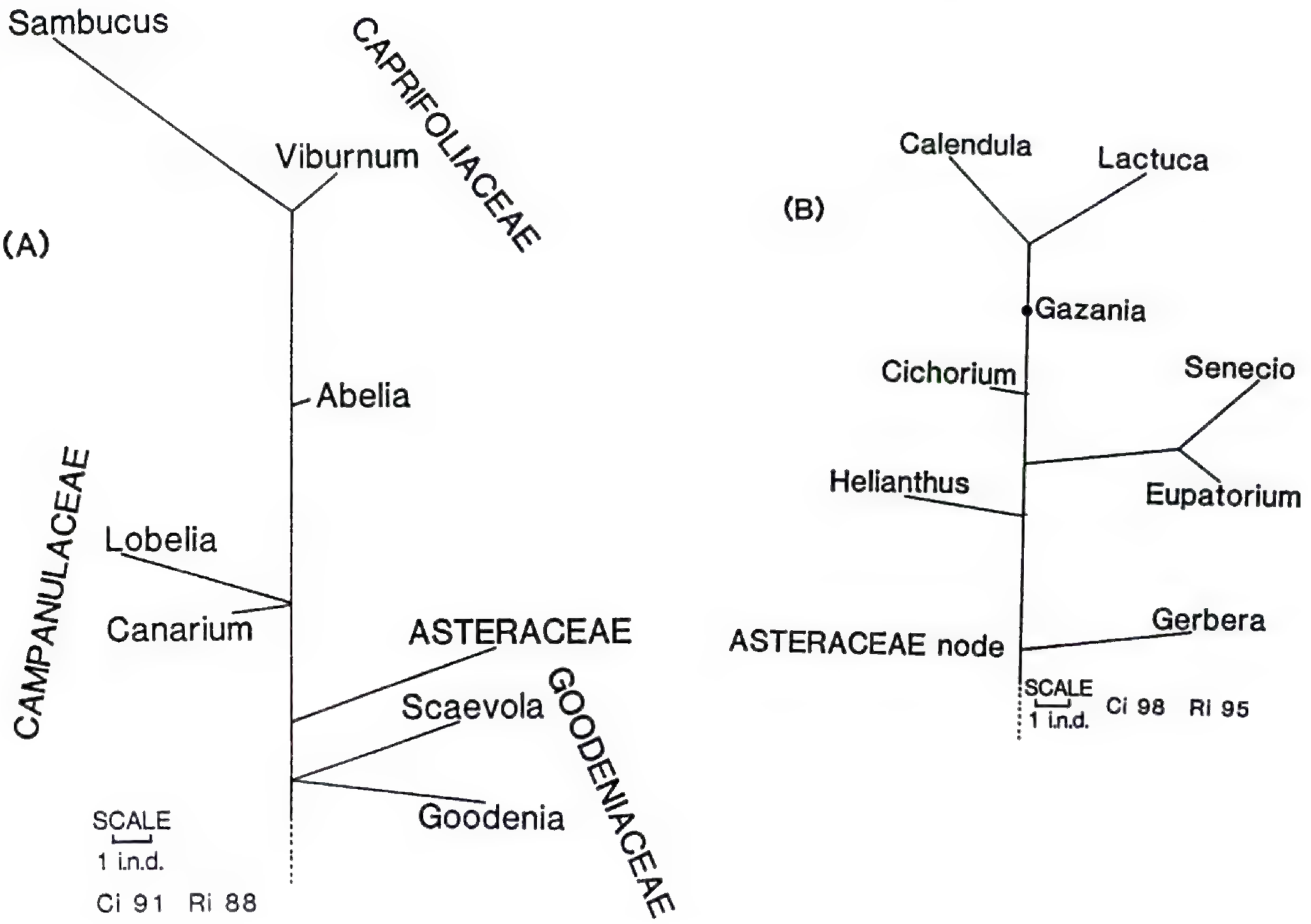


FIGURE 34. (A) Group 26 with node for Asteraceae from (B).

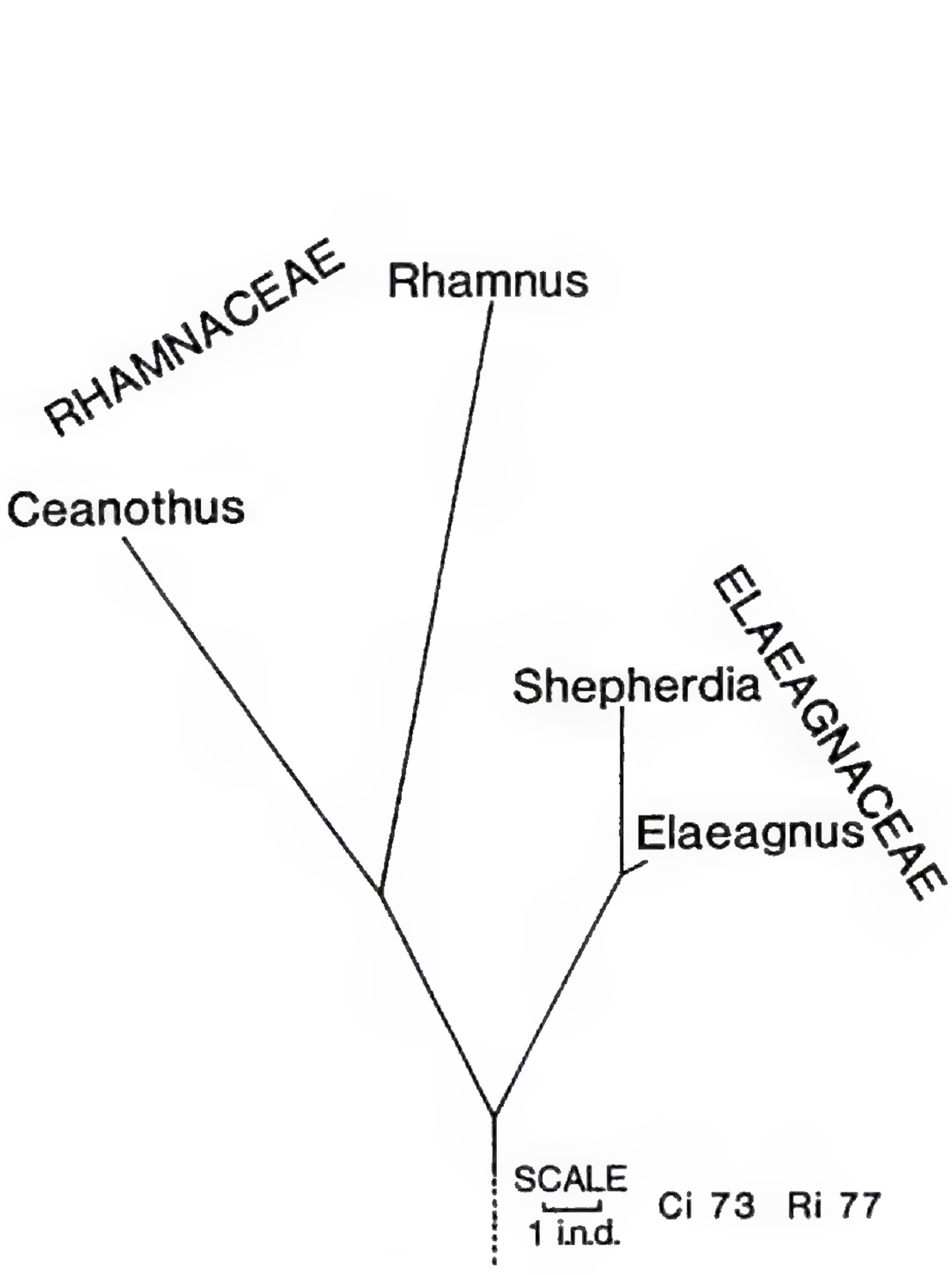


FIGURE 35. Group 27.

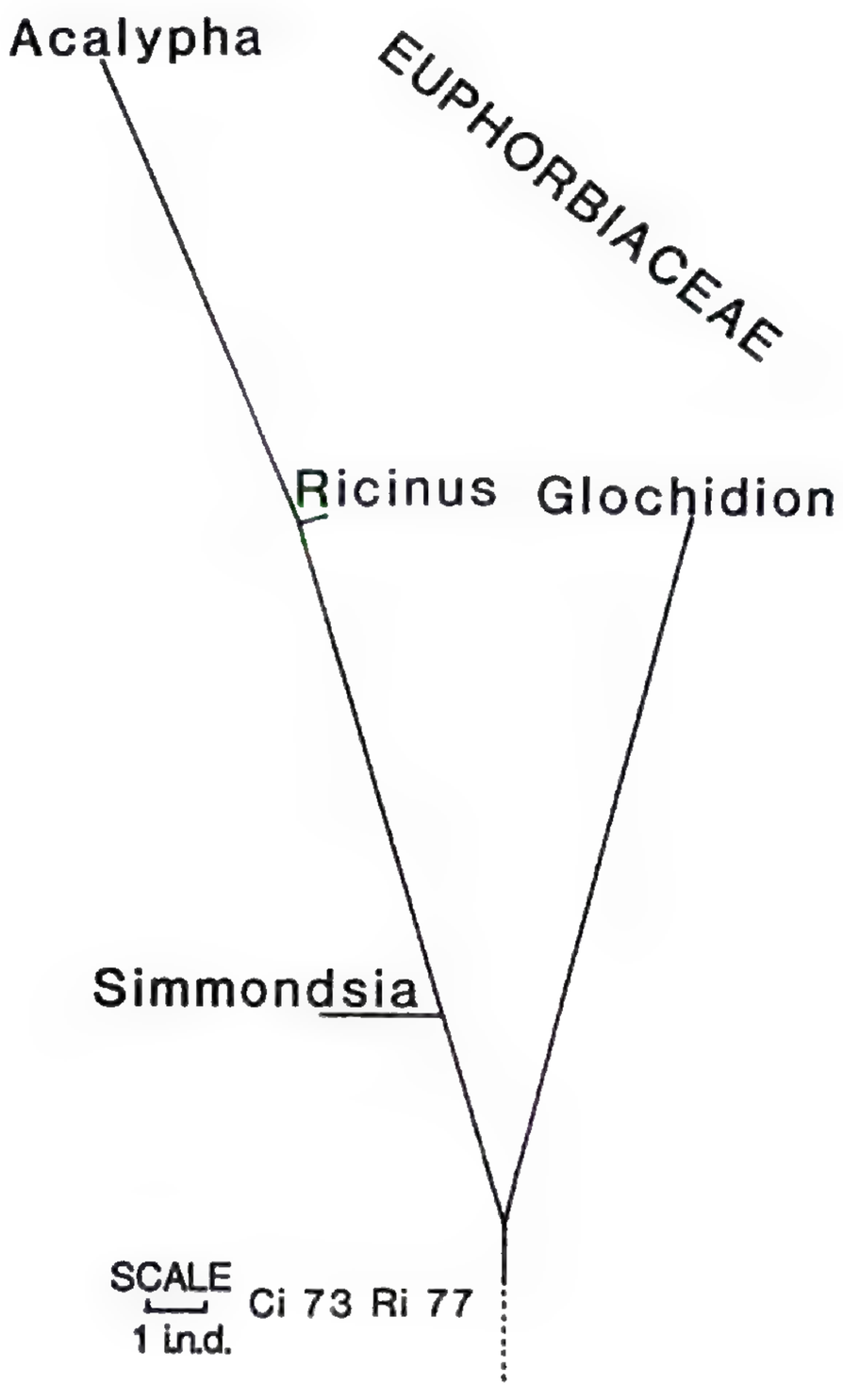


FIGURE 36. Group 28.

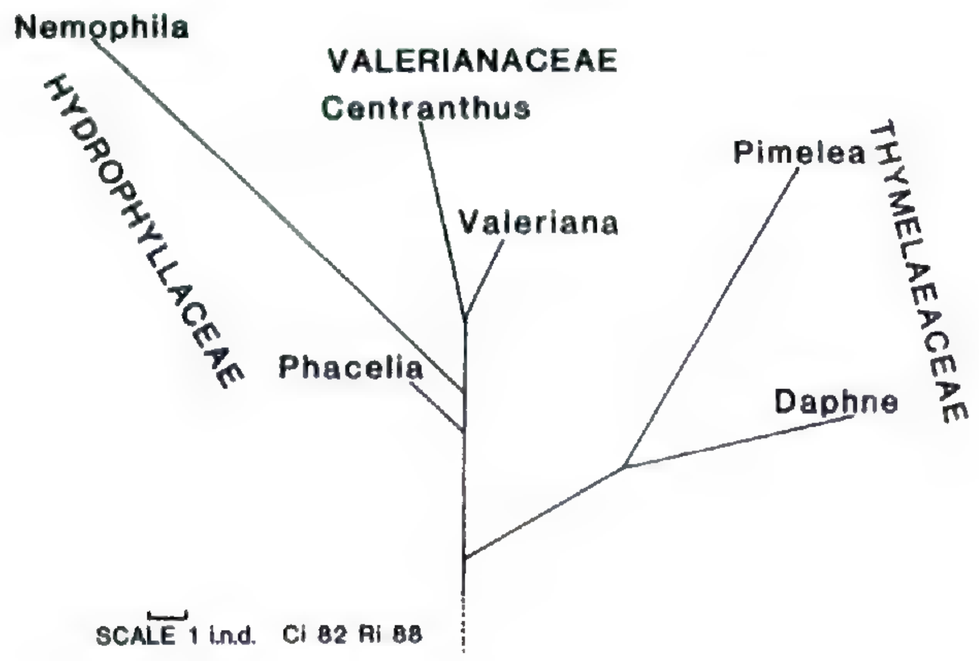


FIGURE 37. Group 29.

fortunate that we failed to obtain a sequence for *Eucnides bartonioides* because this left *Mentzelia* as a singleton and therefore with a "long edge" that joined unreliably. (b) *Plumbaginaceae*. Although the two representatives, *Limonium* and *Plumbago*, paired well, there remained a very long internode joining the family to the tree, and so we have left it unplaced. (c) *Buxaceae*. Originally both *Buxus* and *Simmondsia* were chosen as representatives of Buxaceae (s.l.), but they proved quite different and, since there was taxonomic opinion to support this, they were treated as such. Whereas

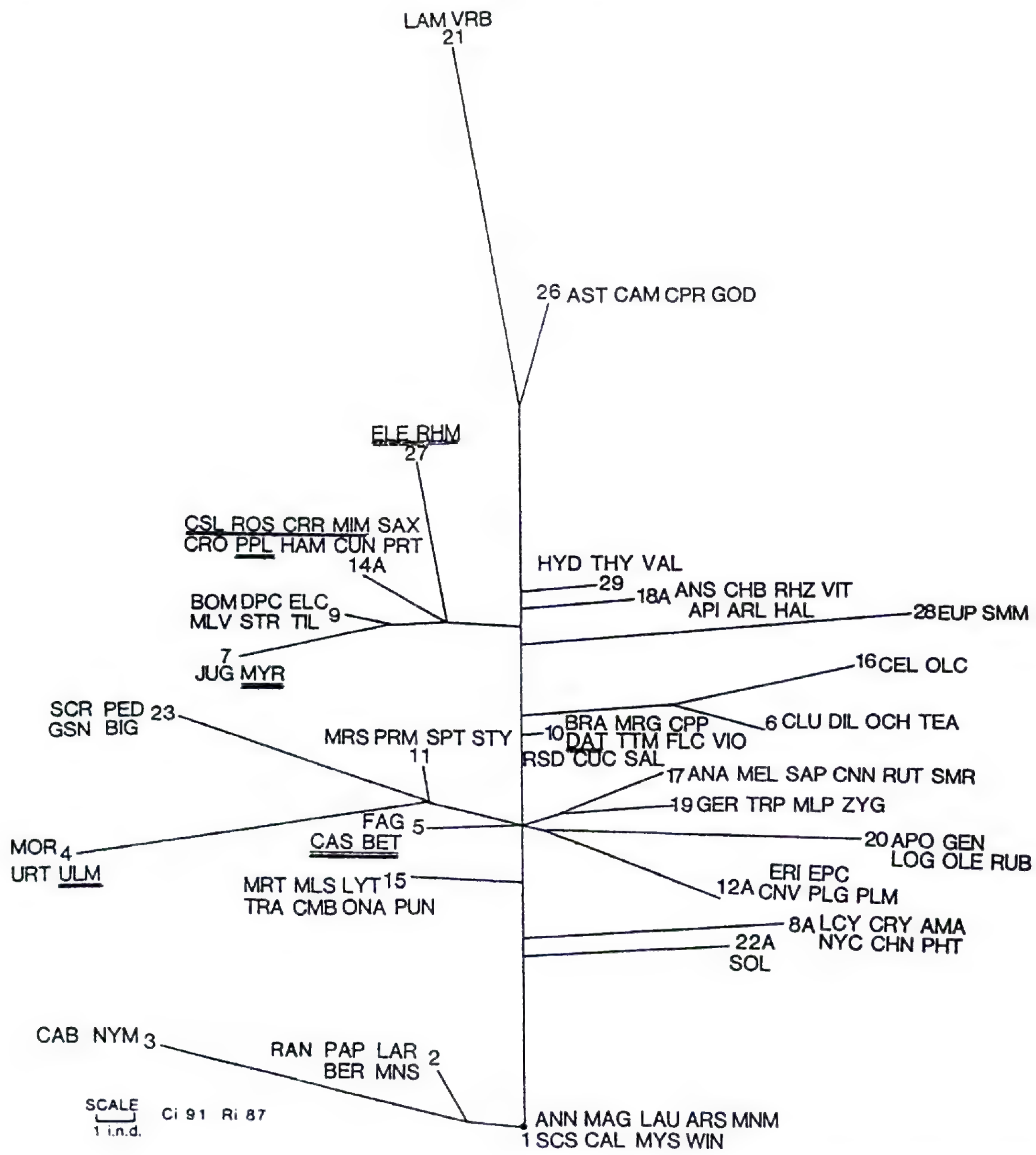


FIGURE 38. The overall tree for the dicotyledons. Groups are numbered and their constituent families indicated using the three-letter acronyms of Weber (1982), given in Table 2. Families in which nitrogen-fixation is known are underlined.

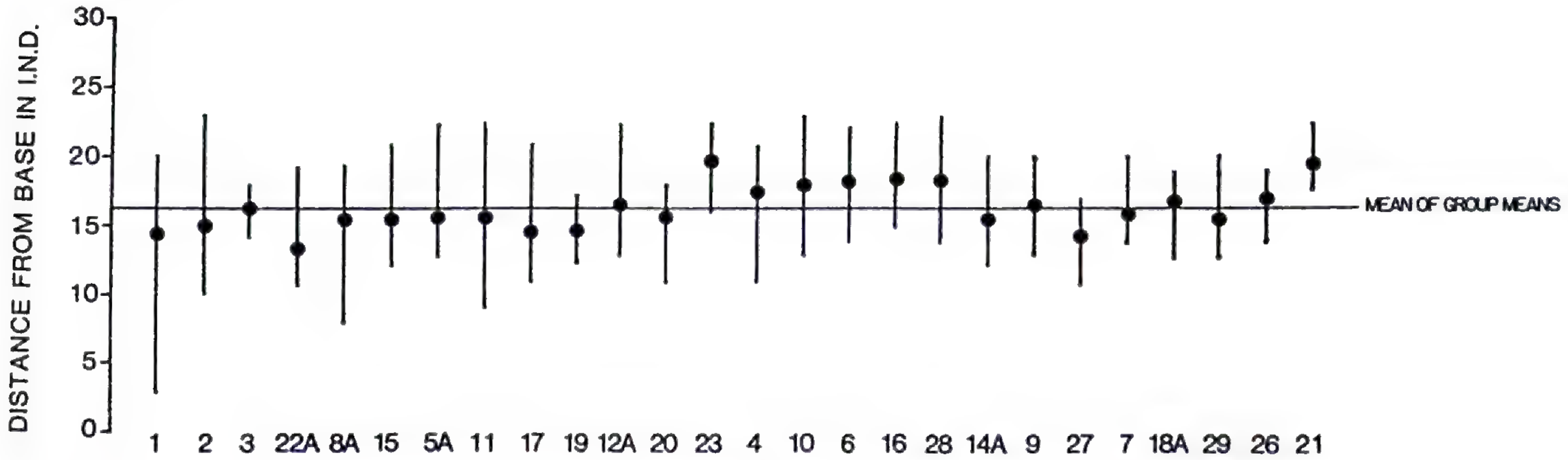


FIGURE 39. Groups are arranged along the X axis in the order that they depart from the trunk of the overall tree (Fig. 38). Solid dots are the mean distances of species of that Group from the angiosperm origin, and bars indicate the range from smallest to greatest.

Simmondsia grouped reasonably well with Euphorbiaceae, *Buxus* did not and remains unplaced.

FIFTH STAGE; THE SIMULTANEOUS ANALYSIS OF REVISED GROUPS

Initially, the nodes of all 26 revised Groups were analyzed using the option *mhennig* followed by *bb*, and the resulting tree was divided into a top, middle, and bottom section. Thus, with overlaps, each contained 14 taxa, a number that could be analyzed using the *ie* option. Fortunately, there was no confusion at the overlaps, and the three parts were fitted together to give the overall tree (Fig. 38).

DISCUSSION

THE RATE OF EVOLUTION AND THE AGE OF THE ANGIOSPERMS

In Figure 38, which shows the overall tree for the dicotyledons, there is a "trunk" from which branches depart at irregular intervals of up to 5 i.n.d. In Figure 39, we arranged Groups in the order that they branch from the trunk. For every species we measured the number of differences (in i.n.d.) between it and the base of the angiosperm tree (Fig. 1). For each Group we show the mean of these distances and also the range from smallest to greatest. The mean of all Groups is 16.2 i.n.d. We have also analyzed variance and shown that there is significant ($P < 0.001$) variation between Groups. Thus, although the difference between a slowly evolving Group such as Group 3 (mean 14.1) and a rapidly evolving Group such as Group 21 (19.7) is not great, it is probably real.

The age of the dicotyledons can be derived from the product of the mean number of differences of species from base and the rate of evolution. Since Figure 6 suggests that the monocotyledons are derived from the dicotyledons this is also the age of the angiosperm. Martin and Dowd (1988) estimated the rate to be 1 i.n.d. in 14 Ma for a single evolutionary line. However, this estimate was based on members of the Fagaceae, Proteaceae, Solanaceae, and Winteraceae, all of which belong to Groups that evolve more slowly than average; their mean number of differences from base is 14.7 i.n.d. Thus, the inferred age of the angiosperms is $14 \times 14.7 = 205$ Ma, that is, at the beginning of the Jurassic. Crane et al. (1989) and Wolfe et al. (1989) have estimated the age of the angiosperms as 200 Ma. If the monocotyledons are indeed derived from the dicotyledons, there is good agreement.

THE RELIABILITY OF OUR TREES

The current limitations of computers and computing programs make it impossible to conduct a large phylogenetic analysis in a completely objective manner. Our first important deviation from objectivity has been accepting taxonomic opinion that species belong to the same family. Our second has been seeking a consensus in placing these into Groups.

The assumption of correct assignment to families is strongly supported by the correct pairing (or formation of clusters of three when appropriate) shown in the objectively derived figures of the final 26 Groups. Of the 95 families with two or three representatives, only 11 had disjunct representatives and, of these, at least four were families sensu lato with taxonomic opinions that they should really be split. These are the separation of *Humulus* from *Morus* in Group 4, of *Flindersia* from other Rutaceae (Group 17), of *Buxus* from *Simmondsia*

(Group 28), and of *Anisophyllea* from other Rhizophoraceae (Group 18). When it is further considered that one aberrant species can disrupt two families, we submit that the high proportion of correct grouping is strong evidence not only for the correctness of other taxonomy at this level but also of the soundness of our approach.

If our methods, while not perfect, are good at the level of placing taxa into families, is there any reason why they should not be equally acceptable at higher levels? We have investigated this with the assumption that the probability of errors will increase as internode lengths decrease. From each of the Group trees we have determined that the average length of internodes within families (restricting the measurements to families with only two correctly paired representatives) is 5.6 i.n.d., while the average length of internodes between families is 4.7. From the final tree showing the relationships of Groups (Fig. 38), the average length of internodes is 3.0. Thus, if our assumption is valid, the ratio 5.6 : 4.7 : 3.0 should reflect the reliability of arranging species within families, families within Groups, and Groups in the final tree. We suggest caution about accepting relationships as the taxonomic level increases.

There is no obvious reason why the ratio just reported should not be similar for other macromolecular sequences. However, with nucleic acid sequencing (see review by Palmer, 1988) the amount of information available might increase by an order of magnitude over that presented here; thus, even if internode lengths at the highest levels are still proportionately small, the probability of errors due to chance when using small numbers should diminish and lead to more decisive phylogenies.

THE VALUE OF THIS STUDY

We believe that the demarcation of plant taxa at all levels should be the prerogative of botanists with a broad background in taxonomy and that the same specialists are best suited to compare the results of this study, expressed as phylogenetic trees, with published phylogenies. Because we do not have that background, we resist the temptation to point out the similarities and differences that we perceive and to assess when our trees are likely to be incorrect. Our perceptions are likely to be unbalanced.

One difference between this phylogenetic study and most others is that it is repeatable. Without detracting from the value of published angiosperm phylogenies, they do seem to depend on the accumulated wisdom and experience of rare individuals whose relevant brain functions are not easily transmitted in entirety. On the other hand, anyone who follows our procedures should arrive at the same phylogenetic trees. More to the point, with improved analytical procedures it is possible that more acceptable endpoints may be reached.

We have avoided the word "conclusions" because we do not claim that this work is definitive. Rather it has led to new working hypotheses which, we hope, others will test with more extensive sampling and more data including much longer sequences. To such investigators our analytical method, whether perceived as successful or not, may be a useful example.

NATURAL SELECTION AND THE EVOLUTION OF RUBISCO-SSU

Under "General remarks about the sequences," we discussed heterogeneity within species and quoted the evidence of Pichersky et al. (1986) that natural selection acts to keep the amino acid sequence constant. Below we present other evidence for the importance of natural selection.

Under "Methods of Data Analysis," we discussed Lake's test, which is based only on transversions (mutations from a purine to a pyrimidine or vice versa) and ignores transitions (purine to purine or pyrimidine to pyrimidine). Lake (1987) quoted evidence (Brown et al., 1982) that in animal mitochondrial DNAs, transitions occur an order of magnitude more frequently than transversions. Zimmer et al. (1989) have found for higher plant cytoplasmic rRNA that, on average, transitions were twice as frequent as transversions with the lowest ratio in the most invariant regions. We have investigated this in 44 families of Groups 1 to 10 and have scored those amino acid changes within families that can be ascribed unequivocally to transversions and transitions. There were 123 transitions and 306 transversions, a proportion of 0.287 transitions and therefore quite different from the evidence just quoted.

We have considered each of the 61 codons in the genetic code and, assuming that each nucleotide can change to another with the same prob-

ability, calculated the frequencies of the four possibilities, i.e., transition causing amino acid change, transversion causing amino acid change, no amino acid change, and lethality (stop). Thus, for the two codons that determine phenylalanine the ratio of transitions to transversions is 0.25, for eight of the amino acids it is 0.33, and the ratio varies from 0.14 to 0.34 with an average of 0.2845. Averaging the 31 variable amino acids in the top line of Table 3 gives the ratio 0.268, which may be compared with the observed figure of 0.287. This suggests that, at the nonsilent positions, which are the only ones we are able to consider, there is close to randomness with respect to the occurrence of transitions and transversions.

We suggest that the large discrepancy between our result and the expectations from chemistry and nucleic acid sequencing is due partly to our inability to score silent substitutions and partly to the overwhelming importance of natural selection in determining the amino acid sequence of an important enzyme. Even though most nucleotide substitutions are presumably transitions, this has little effect on the final outcome, the amino acid sequence, on which natural selection can act.

Other evidence of strong natural selection comes from consideration of variation at positions like 8 and 9. At position 8, 84% of species have glycine and 15% asparagine. This substitution requires at least two nucleotide changes so, in the absence of selection, the single-change intermediates serine or lysine would often be expected, though they have not been observed. Similarly, at position 9, 56% of species have leucine and 28% lysine. Again, this is a two-nucleotide change, but the only single-change intermediates found are methionine and isoleucine, and these are much too rare to occur randomly. Apparently, glycine and asparagine are "adaptive peaks" at position 8 and leucine and lysine are at position 9. When positions 8 and 9 are considered together, there is a small excess over chance expectations of the combinations glycine-leucine and asparagine-lysine; these may be adaptive peaks because both combinations are found within Tiliaceae (Group 9), Papilionaceae (Group 14A), Apocynaceae (Group 20), Proteaceae (Group 14A), and different families of Group 15. Clearly, convergent evolution has occurred.

This last evidence suggests that adjacent positions influence one another, which is known. Another example is probably found in the Onagraceae, the only family with N-terminal phenylalanine and, alongside it, asparagine, again only found in Onagraceae. *Solanum* species with the same rare substitutions at positions 15 and 21 are examples that the effect can extend further. Another example concerns positions 30 and 39, both of which are almost always either valine (V) or isoleucine (I). The frequencies within species of the four possible combinations (VV, VI, IV, II) indicate that the two positions evolve independently; nevertheless, they are different in the monocotyledons, with 67.5% isoleucine, and the dicotyledons, with 35.4% isoleucine. It is conceivable that monocotyledons are richer in isoleucine because they have a more efficient synthetic pathway for isoleucine so that, in the absence of other strong selective forces, the substitution of isoleucine for valine may be favored.

Despite the evidence that natural selection is acting strongly, there are few decisive changes, such as the change from proline to isoleucine at position 6 during the evolution of the monocotyledons. At positions 7 and 8, the combination tyrosine-asparagine occurs in the gymnosperms, Groups 1, 2, and 3, but in no other Groups, suggesting that these amino acids are primitive. However, the distinction between primitive and advanced is usually equivocal; for the following example, normal taxonomic criteria have been used to distinguish 58 primitive genera (those in the gymnosperms, Piperaceae, Nelumbonaceae, and Groups 1, 2, 3, and 5) from 67 advanced genera (those in Asteraceae, Campanulaceae, Goodeniaceae, Hydrophyllaceae, and Groups 10, 20, 21, 22, 23, and 24). At position 12, tyrosine occurred in 5% of primitive and 31% of advanced genera while at position 20 aspartic acid occurred in 5% of primitive and 43% of advanced genera. While admitting that the sampling is not entirely satisfactory, it appears that tyrosine at position 12 and aspartic acid at position 20 are advanced. However, the important point is that the divergence is so indecisive, the primitive amino acids phenylalanine at position 12 and proline at position 20 still occurring in the majority of genera in all advanced Groups.

If it is correct that natural selection acts strongly to determine the amino acid sequence of a protein, this could be important in considering "molecular evolutionary clocks." If the clock that is considered is derived from nucleic acid sequences, the rare event that is the basis of regression of number of

differences on time is nucleotide substitution, the most common form of mutation and not always subject to natural selection. If, however, the clock is derived from amino acid sequences, the rare event is not mutation alone but its incorporation into the gene pool by natural selection. In both cases clocklike behavior is observed, but the rare event is different.

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PHYTOGEOGRAPHICAL RELATIONSHIPS OF THE GENERA OF ANGIOSPERMS IN THE FANJING SHAN MOUNTAIN RANGE, NORTHEASTERN GUIZHOU, CHINA[1]

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ABSTRACT

The Fanjing Shan mountain range, one of six *Man and the Biosphere (MAB) Preserves* in China, covers an area of ca. 567 km² in northeastern Guizhou Province, China. The flora comprises ca. 1,400 species of flowering plants in 636 genera, 23 of which are endemic to China or barely extend into bordering areas. The importance of the 20 largest families, which together contain more than half of the total species, is evaluated, and the phytogeographical affinities of the genera of angiosperms in the flora are analyzed and briefly discussed. In the Fanjing Shan region, tropical and temperate genera are nearly equally represented. The distributional patterns of the genera are analyzed, and some comparisons are made with eight other major mountain regions in south-central and southern China that also contain rich floras of phytogeographical significance. Fanjing Shan is most similar floristically to the Wuyi Shan, Jinfo Shan, and Shennongjia regions, areas to the north and east, than it is to any of the others, which, except for one, are located to the south and west. Besides the tropical and temperate components of the flora, the Fanjing Shan region also contains a rich representation of both Sino-Himalayan and Sino-Japanese elements.

China is particularly rich in numbers of plant species. The estimated 29,000 species of flowering plants and ferns within the country, including about 7,500 indigenous trees and shrubs (Pei, 1984), represent approximately 8–12% of all vascular plants known worldwide. Part of the richness can be accounted for by the diverse geology, complex climatic patterns, and broad altitudinal and latitudinal ranges. Elevational differences in China span more than 9,000 m from the summit of Qomolangma Feng (Mt. Everest) on the border with Nepal at 8,848 m above sea level to 154 m below sea level in the Turpan Depression in the Xinjiang Uygur Autonomous Region. China also occupies the only place on earth where an unbroken transition of vegetational types exists, ranging from tropical rainforests in the south through subtropical, temperate, and boreal forests, to tundra and alpine vegetation in China's southwest and north. This vegetational continuum has resulted in associations of plants not seen in other parts of the world and includes taxa with diverse and widespread phytogeographical relationships extending around the world. Many of the plants in these associations, or their ancestors, are among those considered to have had a much wider distribution during the Tertiary. Fieldwork in the Fanjing Shan mountain range in northeastern Guizhou by Chinese and American botanists in 1986, and fieldwork in other mountain ranges throughout China by Ying and his collab-

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orators, has provided the basis for interpreting the phytogeographical relationships of one particularly rich area, the Fanjing Shan mountain range, located between subtropical and temperate China.

Historical and Botanical Setting

Botanically, Guizhou is one of the least known provinces in China. The province, which occupies an area of about 174,000 km² and reaches from ca. 24°50′ to ca. 29°10′N and from ca. 103°46′ to 109°0′E, is located in a transitional position between the tropics in Guangxi and southern Yunnan and the subtropical and temperate areas of Hunan, Sichuan, and Hubei. The province also occupies a transitional position between the Sino-Himalayan flora, which extends from Yunnan through the Himalayas, and the Sino-Japanese flora of central and eastern China. As such, Guizhou is vital for the analysis and understanding of vegetational and floristic patterns and relationships in all of eastern Asia. Yunnan Province, one of only a few provinces in China for which more or less accurate figures are available, and which borders Guizhou on the west, is reported to contain ca. 14,000 species of flowering plants (Wu, 1984), or nearly half of all the angiosperms in China. Sichuan, to the north, is also considered to be floristically rich, but no accurate figures for the numbers of indigenous plants there are available. Similarly, Guizhou has a rich flora but, again, exact figures are not known.

Until relatively recent times Guizhou was one of the most backward and sparsely populated provinces in China (Geelan & Twitchett, 1974). It is largely mountainous with the major ranges in the north–central and south-central parts of the province. The highest peak, in the Fanjing Shan range in the Wuling Mountains, exceeds 2,550 m elevation (Deng, 1982). Extensive areas of flat land are scarce, and except for narrow areas along major streams, much of the land in cultivation has resulted from terracing. The two major roads in Guizhou roughly divide the province into quarters. One road runs from north to south through the center of the province and the other extends from Hunan Province in the east to Yunnan Province in the west. They intersect in the capital at Guiyang. Minor roads reach most other parts of the province, but travel in Guizhou has always been difficult because of the rugged terrain; even now travel by highway is slow, averaging only about 40 km per hour on the best highways. Because of these factors and the difficulties involved in exploiting the natural resources, the vegetation of Guizhou, although frequently heavily disturbed, is somewhat better preserved than in other parts of China. One exceptionally well conserved region in northeastern Guizhou, the Fanjing Shan mountain range, an area with an unusually rich assemblage of plants and animals, has been designated a *Man and the Biosphere Preserve.*

Few vegetational studies have been conducted in Guizhou. The first was a general discussion on the flora and vegetation of northeastern Guizhou based on observations made in the late summer and fall of 1931 during a collecting trip to the Fanjing Shan region (Steward & Chiao, 1933). Photographs published at the time show the vegetation to be more intact than at present, but signs of drastic disturbance are already evident in some of the photos.

The more recent and most important and extensive vegetational studies in Guizhou were also conducted in the Fanjing Shan mountain region and the findings published in *Scientific Survey of the Fanjingshan Mountain Preserve* by the Fanjingshan Mountain Preserve Institute (1982). Included in this publication are discussions on *Davidia involucrata* Baillon forests (Yang et al., 1982), *Quercus stewardiana* A. Camus (reported as *Cyclobalanopsis stewardiana* (A. Camus) K. M. Lan) forests (Yang, 1983), the general vegetation in the Fanjing Shan region (Huang et al., 1982a), a discussion of soils in the mountains (Zhang & Zhang, 1982), and geomorphology and recent crustal movements (Yang, 1982). Another paper by Huang et al. (1982b) discusses the newly described *Abies fanjingshanensis* W. L. Huang, Y. L. Tu & S. Z. Fang and its forest associations and phytogeographic relationships. The *Davidia* forests are composed of a mixture of deciduous trees with some broad-leaved evergreens and conifers at elevations between 1,000 and 1,800 m on the lower parts of moist slopes. These forests have been described as "complex," and from the descriptions are reminiscent of forests in which *Davidia* occurs in the Shennongjia Forest District in western Hubei Province (Bartholomew et al., 1983). The *Davidia* forests in the Fanjing Shan region have been considered so significant that they have been given government protection. The *Abies fanjingshanensis* forests are among the southernmost *Abies* forests in southeast Asia. According to Huang et al. (1982b) these forests, at 2,100–2,350 m elevation, were first discovered in 1981. The trees grow on north-, northwest-, and northeast-facing slopes with gradients of 50–60°. The species composition and community structure of these forests are somewhat similar to other *Abies* forests in southwest

China, but are reported to differ in a number of characteristics.

The occurrence of five species of *Fagus* L. in Guizhou Province (Guizhou Flora Committee, 1982) is of particular interest and is perhaps the greatest number of species of the genus growing in close proximity anywhere. Three of these species were the subject of investigation in the early 1970s by Tsien et al. (1975; see discussion below), who found that they form distinct forests on Fanjing Shan.

Guizhou is also located near the center of concentration in China of many eastern Asian–eastern North American disjunct genera. Among the taxa belonging to this association in the Fanjing Shan region are *Liriodendron* L. (Magnoliaceae), several species of *Asarum* L. sensu lato, whose affinities appear to be somewhat intermediate between *Asarum* sensu stricto and the eastern North American *Hexastylis* Raf. In the Polygonaceae are several species of *Polygonum* L. sect. *Echinocaulon* Meisner, a section with species in Asia and North America and one species, *P. sagittatum* L., attributed to the eastern part of both continents (Steward, 1930; Park, 1988). Another genus in the Polygonaceae, *Antenoron* Raf. (*Tovara* Adanson in many references), with two species reported for Guizhou, is also frequent and abundant in thickets, moist woods, and along streams. The number of species in the genus is questionable, and the relationship of the Asian taxa to each other and to the single North American species, *A. virginianum* (L.) Roberty & Vautier, is uncertain. Two species of *Liquidambar* L. occur in the Fanjing Shan area, *L. formosana* Hance and *L. acalycina* Chang. Small forests and individual trees of either or both of these two species are rather common in northeastern Guizhou. *Liquidambar acalycina* is considered to be closely related to the North American *L. styraciflua* L. and has been placed in the same section by Chang (1979).

Most recently, a treatment of the vegetation of the entire province has appeared (Huang et al., 1988). This work, which the authors state is aimed at university teachers and students, conservationists, geographers, ecologists, foresters, technicians, and farmers, discusses the physical environment, regionalization of the flora, and main vegetation types and their evolution, and utilization of the forest types in conjunction with farming, forestry, and animal husbandry.

Conservation

Conservation in China has recently been given high priority, and it is particularly noteworthy that the Fanjing Shan mountain range and forests have been designated a *Man and the Biosphere Preserve*. Unfortunately, however, habitat destruction is taking place at a rapid rate throughout China and even Fanjing Shan is not being spared. Trees around the margins of the preserve are actively being cut for conversion to charcoal, which is then transported several kilometers to villages at lower elevations, where it is sold. Other selected trees are being cut throughout much of the easily accessible parts of the preserve to build houses and for other construction purposes. The herbaceous flora suffers from the activities of overzealous diggers of medicinal plants who sell their harvests in all of the larger cities and towns surrounding Fanjing Shan. Tourism is being encouraged, and while most tourists remain close to the trails, their numbers are becoming so great that they are having a very definite and negative impact on many of the areas they visit. Their presence has become even more noticeable with the introduction and spread of nonbiodegradable food and beverage containers throughout China over the past few years. The lack of adequate sanitary facilities will undoubtedly have a deleterious effect on water resources. Unless these threats to the integrity of the area are addressed in the very near future, the Fanjing Shan region will ultimately resemble much of the rest of rural China, and many species of both plants and animals will be lost locally, if not completely.

Geographical Limits, Soil Types and Climate

The Fanjing Shan mountain range is generally known to include the highest peaks in Guizhou province. It is centered between 27°49′50″ and 28°1′30″N latitude and 108°45′55″ and 108°48′30″E longitude in northeastern Guizhou. The area is deeply cut on all sides by five deep, V-shaped valleys, resulting in a steep topography. The highest peak is about 2,570 m above sea level, and the relative elevation over the surrounding countryside ranges from 1,000 to 2,000 m. Four major soil types have been described in this region: (1) yellow-red earth, below 700 m; (2) yellow earth, (500–)700–1,400 m; (3) yellow-brown earth, 1,400–2,000 m; (4) mountain brown podzolic soil, above 2,200 m. All exhibit an acid reaction, with pH values lower than 5.0. Zhang & Zhang (1982) also reported a soil type, which they call a dark, mountain thicket soil, different from the mountain yellow brown earth and the soil in shrub meadows, in a zone between 2,000 and 2,300 m.

An analysis of the climatic features of the Fan-

jing Shan mountain area was made by Wang (1982), who classified the vertical climatic zones as middle subtropical, northern subtropical, southern temperate, and middle temperate.

On the basis of these floristic, vegetational, and environmental studies in the Fanjing Shan mountain range, we are now able to draw some conclusions on the relationships of its highly diverse and interesting flora and to discuss to some extent the phytogeography of an important segment of the Chinese flora.

Composition of the Vegetation in the Fanjing Shan Mountain Range

There are five forest zones from the base to the crest of the Fanjing Shan mountain range: (1) evergreen broad–leaved forest zone (below 1,300 m); (2) mixed evergreen-deciduous broad-leaved forest zone (1,300–1,900 m); (3) deciduous broad-leaved forest zone (1,900–2,100 m); (4) subalpine coniferous forest zone (2,100–2,350 m); and (5) subalpine shrub and meadow zone (above 2,350 m). The dominant genera in the forests are *Castanopsis* (D. Don) Spach, *Quercus* L., *Fagus*, *Acer* L., *Rhododendron* L., and the gymnosperm genera, *Tsuga* Carr. and *Abies* Miller, while the dominant members of the subalpine shrub-meadow zone are *Rhododendron* spp., *Sinarundinaria chungii* (Keng) P. C. Keng, and *Arundinaria fangiana* C. Camus. Because the zone occupied by the latter association is so narrow, it is not an important floristic component of the Fanjing Shan range. The distribution of the dominant species in the other zones is as follows.

Evergreen Broad-Leaved Forests

The dominant species of this forest type are *Castanopsis tibetana* Hance, *C. eyrei* (Champion) Tutcher, *C. fargesii* Franchet, *C. carlesii* Hayata, *Quercus stewardiana*, *Q. englergiana* Seemann, and *Q. dentata* Thunberg var. *oxyloba* Franchet. Almost all of the dominant species have distributions south of the Chang Jiang (Yangtze River) and are concentrated in central-southeastern China. *Castanopsis fargesii*, *C. carlesii*, and *C. eyrei* extend to Taiwan.

Deciduous Broad-Leaved Forests

The deciduous broad-leaved forests contain the primary portion of the Fanjing Shan flora. The dominant members of the forests are *Fagus lucida* Rehder & Wilson, *F. longipetiolata* Seemann, *F. engleriana* Seemann, and *Acer flabellatum* Rehder. The range of distribution of *Acer flabellatum* includes northeastern Yunnan, eastern Sichuan, western Hubei, northern Guangxi, northwestern Jiangxi, and Guizhou, an area where *Acer* is richly represented.

The three species of *Fagus* were the subject of investigation in the early 1970s by Tsien et al. (1975), who found that they form distinct forests on Fanjing Shan. Each of the species is segregated according to slope exposure, with *Fagus lucida* on west- and east-facing slopes, *F. engleriana* on north-facing slopes, and *F. longipetiolata* on south-facing slopes. Paleopalynological studies reveal that these *Fagus* communities have been in a continuous state of flux in response to changes in climatic conditions and that the three species have occupied various positions in relation to each other as climates differed in the past (Kong et al., 1977). The present distribution of these three species of *Fagus* in the Fanjing Shan region corresponds to their latitudinal distribution, where *F. longipetiolata* is a more southern species, *F. engleriana* is northern, and *F. lucida* is a more centrally distributed plant.

Subalpine Coniferous Forests

Among the important species in this forest type are *Tsuga forrestii* Downie, *T. longibracteata* Cheng, and *Abies fanjingshanensis*, with sporadically intermixed deciduous broad-leaved trees. Of the two species of *Tsuga*, one occurs in southern Sichuan, northwestern Yunnan, and western Hubei; the other extends from northeastern Guizhou through southern Hunan, northern Guangxi and Guangdong to Fujian. The distributional areas of these two species overlap in the Fanjing Shan and adjacent regions (Fig. 1). *Abies fanjingshanensis*, undoubtedly a relict species, is endemic to Fanjing Shan at elevations between 2,100 and 2,350 m. As with the examples mentioned above, we find that nearly all of the dominant species in the flora of Fanjing Shan are endemics concentrated in central and southeastern China.

Survey of Larger Families of Angiosperms

The largest families of flowering plants in the Fanjing Shan mountain range are the Rosaceae (66 species), Poaceae (54 species), and Fabaceae (51 species) (Table 1). The Rosaceae are a major family in this region and are very characteristic of the flora and vegetation of temperate areas in China. Poaceae and Fabaceae also exhibit an extraordinary frequency in forests and elsewhere in this

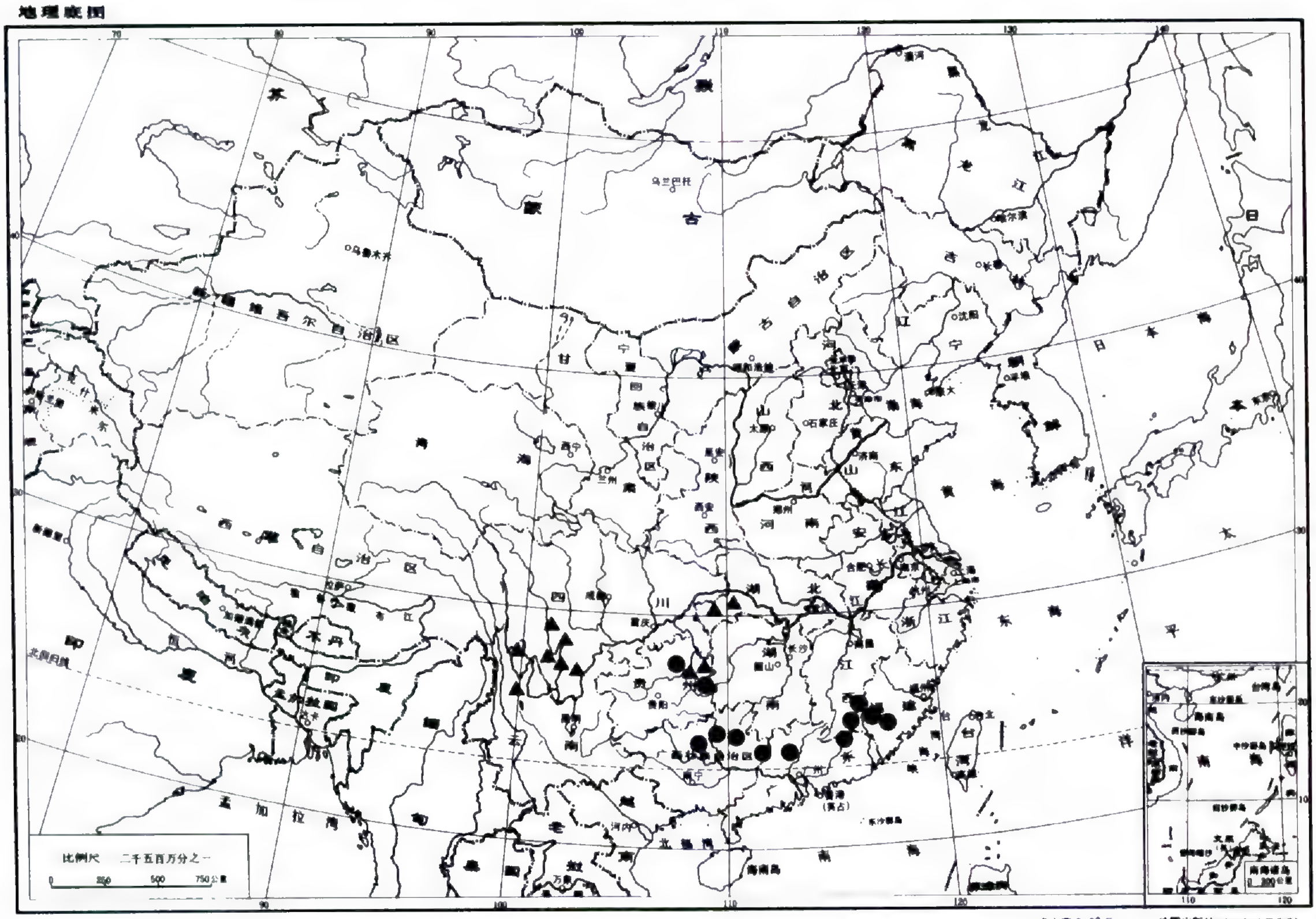

FIGURE 1. Distribution of *Tsuga forrestii* (▲) and *T. longibracteata* (●). Note overlap in their ranges in the Fanjing Shan region.

region. The development of the Fabaceae is mainly in the Papilionoideae, which has 41 species, while the Mimosoideae and Caesalpinioideae have only 2 and 8 species, respectively.

There are three families with between 40 and 50 species: the Liliaceae (48 species), Asteraceae (45 species), and Lauraceae (41 species). The Liliaceae and Orchidaceae form the major part of the wealth of the petaloid monocots, and together comprise nearly 9% of the total flora. The Lauraceae, with some 41 native species, comprise an important element of the flora. This family is tropical in nature, and even most genera in temperate regions have their distribution centers in tropical or subtropical locations.

There are five families with between 30 and 40 species. They are the Orchidaceae (38 species), Lamiaceae (36 species), Fagaceae (33 species). Cyperaceae (33 species), and Ericaceae (30 species). The 33 species in 6 genera in the Fagaceae are important elements in the flora. Many members of the family, especially species of *Castanopsis*, *Lithocarpus*, and *Quercus*, are the dominant forest species, and *Fagus*, with five species in China and three on Fanjing Shan, is centered and well developed in this region. Two families, the Ericaceae and Lamiaceae, are relatively poorly represented, but three genera of Lamiaceae endemic to China (*Bostrychanthera* Bentham, *Hanceola* Kudo, and *Rostrinucula* Kudo) occur here. The above 11 families comprise nearly 34.8% of the species of flowering plants in the Fanjing Shan flora.

There are nine families with between 20 and 30 species. In order of size they are: Ranunculaceae (29 species); Apiaceae (29 species); Theaceae (28 species); Saxifragaceae (28 species); Scrophulariaceae (24 species); Rubiaceae (24 species); Vitaceae (22 species); Caprifoliaceae (21 species); and Celastraceae (21 species). Except for the Theaceae, Rubiaceae, and Vitaceae, these families are north and south temperate, or only north temperate, in distribution.

The large number of archaic families in the flora of Fanjing Shan should also be mentioned. Their presence may be explained by the antiquity of the flora, although they are always represented by only one or a few species. The polycarpic Magnoliidae, generally considered to comprise the most primitive families and genera of flowering plants (Cronquist, 1981), are distributed mainly in eastern and southeastern Asia and in North, Central, and northern South America; there are 13 species in 8 genera

TABLE 1. Ranking of families in the Fanjing Shan flora based on numbers of species.

	Number of genera[1]	Number of genera endemic to China	Number of species[2]	Number of species endemic to China	
1. Rosaceae	14/48		66/855	51	
2. Poaceae	41/228		54/1,202	8	
3. Fabaceae	33/163		51/1,252	22	22.3%
4. Liliaceae	21/55		48/335	25	
5. Asteraceae	41/227	1	45/2,323	8	
6. Lauraceae	8/20		41/422	24	34.8%
7. Orchidaceae	29/165		38/998	13	
8. Lamiaceae	20/99	3	36/808	16	
9. Cyperaceae	9/31		33/668	6	
10. Fagaceae	6/6		33/281	22	
11. Ericaceae	7/14		30/718	21	
12. Ranunculaceae	12/40		29/736	14	
13. Apiaceae	15/95		29/525	11	
14. Theaceae	6/7		28/397	18	
15. Saxifragaceae	14/26		28/440	19	
16. Scrophulariaceae	12/60		24/634	10	
17. Rubiaceae	19/75	1	24/477	13	
18. Vitaceae	6/7		22/109	12	
19. Caprifoliaceae	5/12		21/207	17	
20. Celastraceae	5/13		21/184	12	
Total	322/1,398		701/13,571	342	
Percentages	50.2%		50.1%/46.73%	48.9%[3]	

[1] Number of genera in Fanjing Shan/number in China.
[2] Number of species in Fanjing Shan/number in China.
[3] Percentage of total species of larger families in Fanjing Shan region.

(*Illicium* L. (Illiciaceae) *Liriodendron* L., *Magnolia* L., *Manglietia* Blume, *Michelia* L. (Magnoliaceae), *Kadsura* Jussieu and *Schisandra* Michaux (Schisandraceae), and *Tetracentron* Oliver (Tetracentraceae)), in this category within the Fanjing Shan area. The Hamamelidaceae are also thought to be an archaic group; in the Fanjing Shan region the family is represented by 13 species in 6 genera. The main families of the old "Amentiferae," such as the Betulaceae, Fagaceae, Juglandaceae, Moraceae, Salicaceae, and Ulmaceae, are found on Fanjing Shan. In addition, three families endemic or nearly endemic to China, and also considered to be primitive or relictual, the Davidiaceae, Eucommiaceae, and Sargentodoxaceae (also in northern Laos and Vietnam), are also found here. The Fanjing Shan mountain range therefore harbors a great number of archaic or primitive taxa regardless of the criteria on which they are based.

The combined families mentioned above contain 701 species, or 51.1% of the total flora, and play an important role in shaping the characteristics of the forests of the Fanjing Shan mountain range.

RELATIONSHIPS OF THE FANJING SHAN FLORA

A. GEOGRAPHICAL AFFINITIES OF THE GENERA

The Fanjing Shan mountain range is very rich in genera of flowering plants, with 636, but is not especially rich in numbers of species, with only 1,431 (2.25 species per genus). Based on the geographical distribution given for each genus in Willis's (1973) *Dictionary of the Flowering Plants and Ferns* (eighth edition), and Mabberley's (1987) *The Plant-book*, and supplemented by information gathered from specimens in the herbaria at A, GH, HGAS (Guizhou Academy of Sciences), Guizhou Normal University, and PE, we were able to classify the genera of flowering plants in the Fanjing Shan preserve into 14 distribution types (Table 2) as follows.

1. Cosmopolitan genera

Some genera, mainly aquatics and mesophytes, are so widespread that they can be classified as

TABLE 2. Distribution types of genera of seed plants in the Fanjing Shan region.

Distribution type	Number of genera in the region	Percentage of all genera in the region	Number of species in the region	Percentage of all species in the region	Number of genera in China with this distribution pattern	Percentage of all genera in China with this distribution pattern
Cosmopolitan	56	8.8	162	11.3	107	52.3
Pantropic	109	17.1	291	20.3	373	29.2
Tropical America and tropical Asia	11	1.7	34	2.4	96	11.5
Old World tropics	36	5.7	63	4.4	162	22.2
Tropical Asia and tropical Australia	29	4.6	48	3.4	152	19.1
Tropical Asia and tropical Africa	23	3.6	31	2.2	160	14.1
Tropical Southeast Asia	60	9.4	114	8.0	570	10.5
North Temperate	112	17.6	332	23.2	297	37.7
Eastern Asia and North America	46	7.2	114	8.0	120	38.3
Old World Temperate	31	4.9	54	3.8	163	19.0
Temperate Asia	6	0.9	13	0.9	58	10.3
Mediterranean, western Asia and central Asia	1	0.2	1	0.07	169	0.6
Eastern Asia	93	14.6	149	10.4	294	31.6
Chinese endemics	23	3.6	25	1.7	214	10.7
Total	636	99.9	1,431	100.07	2,935	21.7

cosmopolitan. Fifty-six genera fall into this category. These taxa belong to 31 of the 143 native families in the Fanjing Shan region and include 162 species. These cosmopolitans comprise about 8.8% of the flora of Fanjing Shan, and 21.7% of the total families.

Many mesophytes such as *Senecio* L., *Aster* L., *Geranium* L., *Ranunculus* L., *Carex* L., *Polygonum* L., *Galium* L., and *Cyperus* L. are the dominant species of the herbaceous layer in forests and in montane grasslands. Because information derived from the distribution of cosmopolitan genera makes it impossible to determine the geographical affinities of the flora of the Fanjing Shan range, they are excluded from the statistical data.

2. Pantropical genera

Genera found in all three tropical regions (the Americas, Africa–Madagascar, Asia–Australasia) may be considered pantropical. A typical example is *Hypoxis* L. Other pantropical genera are concentrated in the tropics of one continent, but have few species in one or both of the other two regions. As an example, *Nertera* Banks & Solander ex Gaertner contains about 12 species, one common to New Zealand, South America, and Tristan da Cunha, one on Tristan da Cunha, one in Australia, one in Chile, one on Granada, two in the Philippines, one in south China, and eight in New Zealand (van Steenis, 1962; Wu & Li, 1965). Although the distribution of the genus might argue for the existence of *Nertera* before the breakup of the southern landmass, a more reasonable explanation is that members of the genus have been dispersed more recently by migrating birds that eat the berry fruits.

In the Fanjing Shan region 109 genera, or approximately 17.1% of the total genera (excluding the cosmopolitan ones), may be classified as pantropics. They contain about 291 species, which is 20.3% of all species in the flora of Fanjing Shan.

Of the 109 pantropical genera in Fanjing Shan, about 52 (47.7%) are herbaceous 42 (38.5%) are woody, 4 (3.7%) consist of lianas, and 11 others include both herbaceous and woody species. Although the distribution centers of these genera are primarily concentrated in the tropics of both hemispheres, a few of them, such as *Ilex* L., *Cynanchum* L., *Impatiens* L., *Buddleja* L., *Celastrus* L., *Cuscuta* L., *Euphorbia* L., *Indigofera* L., and *Grewia* L., extend to subtropical or even temperate regions.

3. Tropical America and tropical Asia

This distribution type is represented by proportionally few genera, especially when compared to those with a pantropical distribution. Only 11 genera in 10 families, representing only 1.7% of the total genera, are included in this category. These genera, all of which are woody, contain 34 species,

or 2.4% of the total flora of Fanjing Shan. In Australasia some of these genera may extend to northeast Australia or the southwest Pacific Islands, but their distribution centers are always limited to the American and Asian tropics. In China, several genera extend into temperate regions, e.g., *Picrasma* Blume, *Sageretia* Brongniart, and *Lindera* Thunberg, the latter to Liaoning province at lower elevations. All three, however, are concentrated in south-southwest China. Similar examples are found in *Litsea* Lamarck, but the genus attains its greatest diversity in southern and southwestern China, which has been considered to be its place of origin (Li, 1979). In North America, *Lindera* extends into the New England states and just reaches southern Canada; *Litsea* is found as far north as southeast Virginia and Tennessee. The American members of these two genera may not, therefore, be considered strictly tropical. These genera are common in the Fanjing Shan region and many of their species are the main constituents of the evergreen and deciduous broad-leaved forests.

4. Old World tropics

This distribution type is difficult to separate from the subtropical and sometimes even temperate pattern. We have segregated these genera mainly on the degree of their concentration in the tropics of the Old World. An example is *Dopatrium* Buchanan-Hamilton ex Bentham, which has about 12 species in the Old World tropics (Mabberley, 1987), but only one species, which extends as far north as Henan province, in China. Within the flora of Fanjing Shan, 36 genera (5.7%) may be classified as Old World tropical. Of these, 14 (38.9%) are woody, 14 (38.9%) are herbaceous, 3 (8.3%) are lianoid and 5 genera have both woody and herbaceous species. Among them, *Pittosporum* Banks ex Gaertner, *Albizia* Durazzini, and *Mallotus* Loureiro are constituents of broad-leaved forests, while others such as *Maesa* Forsskal and *Embelia* Burman f. are also rather common, but only in the shrub layers of the forests.

5. Tropical Asia and tropical Australia

In one sense this category is a subset of the Old World tropical pattern in that it includes genera with much the same kind of distribution, but with the main areas of concentration in the eastern and southeastern portion of the Old World tropics rather than in the west. The western extremity of this distribution type extends to Madagascar, but not to the African mainland. An example is found in *Balanophora* Forster & G. Forster in which 80 species occur in Australia, Polynesia, Malaysia, South China, Japan, and Madagascar, but none occur on the African continent.

Twenty-nine genera (4.6% of all genera) and 48 species (3.4% of all species) can be placed in this category. Among the genera, 10 are woody, 14 are herbaceous, and 5 are lianoid; only one genus (*Dunbaria* Wight & Arn.) has both woody and herbaceous species. The genus *Microcarpaea* R. Brown, with only one species, is a typical representative of this distribution type. In China these genera occur predominantly in southern China, but a few of them enter the temperate zone. Some, such as *Elaeocarpus* L., *Toona* (Endlicher) M. Roemer, *Wikstroemia* Endlicher, and *Nothopanax* Miquel, are important constituents of subtropical forests and shrublands. *Nothopanax* has a disjunct distribution in southwest China and New Zealand.

6. Tropical Asia and tropical Africa

This category is also a subcategory of the Old World tropical pattern in that it includes genera with much the same kind of distribution, but with their centers of concentration in the west and southwest rather than in the east. The eastern extremity of this distribution type extends to Fiji in the South Pacific, but not to Australia. A good example of this pattern is seen in *Lecanthus* Wedd., where three species occur in tropical Asia, one in tropical Africa, and one in Fiji, but none occur in Australia. A similar example is found in *Girardinia* Gaudichaud-Beaupre, which also extends into subtropical to temperate China. The genus *Crassocephalum* Moench contains 30 species, 29 of which are restricted to Africa and Madagascar, but one aggressive species occurs in eastern Asia.

In the Fanjing Shan region, 23 genera (3.6% of the total) belong to this distribution type. These genera contain 31 species (2.2% of the total species). Among the genera, 6 are woody, 10 are herbaceous, 3 are lianoid, and 4 contain both woody and herbaceous members. Except for *Debregeasia* Gaudichaud-Beaupre and *Miscanthus* Andersson, all of them are uncommon in this region. The monotypic genus *Toddalia* Jussieu is a typical representative of this distribution type.

7. Tropical southeast Asia

The Indo-Malesian region has one of the richest floras in the world. The eastern portion of the Indian region, and the northwestern portion of the Malesian region, through the Malay and Indochinese peninsulas, are very closely linked floristically with the mountains of south-central China.

Thus, a fairly large number of "typical" Indo-Malesian genera occur in south China. In the Fanjing Shan region, 60 of the 636 genera (9.4%) are included in this category. These genera contain about 114 species and constitute 8.0% of all the species in the flora. Among these 60 genera, 33 (55%) are woody, 17 (17%) are herbaceous, 6 (10%) are lianoid, and only 4 genera contain both woody and herbaceous species. Some of the woody genera, such as *Phoebe* Nees, *Machilus* Nees, *Neolitsea* (Bentham) Merrill, *Camellia* L., *Schima* Reinwardt ex Blume, and *Adinandra* Jack, *Daphniphyllum* Blume and *Carrierea* Franchet are the main constituents of evergreen, deciduous, and mixed broad-leaved forests in the Fanjing Shan area. *Ophiorrhiza* L. and *Dichroa* Loureiro are rather common in the herb and shrub layers of these forests.

8. North Temperate

Included under this heading are all the widely distributed genera restricted to the temperate regions of Eurasia and America. There are also a few genera that are equally characteristic of North Temperate areas and parts of the tropics, especially in the more mountainous regions of the latter. For example, the genus *Vaccinium* L. is widespread in temperate Eurasia and America, but some species extend into tropical regions of Asia and America, especially into tropical mountainous regions. Other examples are *Juglans* L., *Cotoneaster* Medikus, *Artemisia* L., *Rosa* L., *Thalictrum* L., and *Sambucus* L. In the Fanjing Shan area the genera belonging to this category total 112, or 17.6% of the total genera enumerated. They represent the highest proportion of distribution types in the flora of Fanjing Shan. These genera contain over 330 species, nearly 25% of all species in this area. Among them are 42 woody and 64 herbaceous genera, 8 genera with both woody and herbaceous species, and only 1 lianoid genus.

This category forms the nucleus of the flora of the Fanjing Shan mountain range. Among the especially prominent and significant genera in terms of their dominance in the vegetation of the region are *Acer*, *Fagus*, *Betula* L., *Carpinus* L., *Alnus* Miller, *Cornus* L., *Castanea* Miller, *Juglans*, *Sorbus* L., *Prunus* L., *Tilia* L., *Rhododendron*, *Ilex*, and *Fraxinus* L. Most of these genera contain only deciduous trees and all of them are typical North Temperate genera. Within this category, however, 17 of the 112 genera occur disjunctly in both North Temperate and South Temperate regions, while *Coriaria* L., a common shrub genus, shows a discontinuous distribution in the Mediterranean area, eastern Asia from the Himalayas to Japan, New Zealand, Mexico, and Chile.

9. Eastern Asia and North America

Among North Temperate disjunction patterns, the one between eastern Asia and North America is perhaps the most important biogeographically for the amount of interest it has generated. It has been one of the best known since Asa Gray (1846) first drew special attention to it, and it has been much studied and discussed (Boufford & Spongberg, 1983; Graham, 1972a, b; Hara, 1952, 1956, 1972; Hu, 1935, 1936; Li, 1952; Wu, 1983).

In the flora of Fanjing Shan 46 genera, which represent 7.2% of the total genera, belong to this distribution type. These genera contain 114 species, or 8.0% of all species in the region. Among these genera, 23 (50% of this distribution type) are woody, 17 (37%) are herbaceous, 4 (8.7%) are lianoid, and only 2 genera (4.3%) have both woody and herbaceous species. Although genera with this distribution pattern are concentrated in eastern Asia and North America, some of them (such as *Itea* L., *Nyssa* L., *Castanopsis*, and *Lithocarpus*) extend into the Indo-Malesian region, or occasionally even into Central Asia (*Veronicastrum* Moench), or Australia (*Lespedeza* Michaux) in the Old World, and into tropical regions in the New World (*Catalpa* Scopoli, *Muhlenbergia* Schreber, and *Illicium*). *Tsuga* and *Castanopsis* are important constituents of hemlock forests and broad-leaved evergreen forests, respectively. *Lithocarpus*, *Liquidambar*, *Hydrangea* L., *Illicium*, *Sassafras* Nees & Ebermaier, *Photinia* Lindley, and *Aralia* L. are also major constituents of evergreen and broad-leaved deciduous forests in this region. Two additional genera, *Abelia* R. Brown and *Cleyera* Thunberg, are also rather common; they are disjunctly distributed in eastern Asia and Mexico.

10. Old World Temperate

Discussed here are genera widely distributed over the North Temperate Zone of the Old World. At both ends of their range, and more especially in the west, many of these genera, such as *Dipsacus* L., *Inula* L., *Lactuca* L., *Lotus* L., *Oenanthe* L., and *Peucedanum* L., often show a tendency to extend southward into Africa. Two additional genera, *Ligustrum* L. and *Daphne* L., although they range throughout the Old World Temperate Zone, may also be mentioned here because, respectively, they also have one or a few species in Australia and in the Indo-Malesian region.

In the flora of Fanjing Shan, 31 genera, or 4.9% of all genera, belong to this distribution type. These

genera contain 54 species, or about 3.8% of the total. Among the genera, 6 are woody, 22 are herbaceous, and only 3 have both woody and herbaceous members. The woody genera are not the main constituents of the forests of Fanjing Shan, but the herbaceous genera are the main constituents of the montane grasslands or of the herb layers of the forest.

11. Temperate Asia

This type is represented by proportionally few genera, especially when compared with the North Temperate type. Included here are all the genera mainly distributed in Temperate Asia. Their distributional areas sometimes extend southward to the more elevated regions of the subtropical zone. For example, *Campylotropis* Bunge (Fabaceae) contains about 45 species, of which 29 are distributed in China, and almost all of which are concentrated in the subtropical regions of the country (Fu, 1987). These species show their temperate nature, however, in their ecologically restricted occurrence to areas with elevations between 1,000 and 3,000 m. We have segregated this group of genera mainly on the basis of the ecological preference of their subtropical representatives.

In the flora of Fanjing Shan this distribution type is represented by only 6 genera, or 0.9% of all genera. Together they contain about 13 species, which comprise only 0.9% of all species. With the exception of one woody genus, *Campylotropis*, all are herbaceous.

12. Mediterranean, western Asia to central Asia and China; North America to Central America

In the flora of Fanjing Shan, only *Pistacia* L. belongs to this distribution type.

13. Eastern Asia

This category is a large one calculated to contain about 93 genera (14.6% of the total) and is rather difficult to distinguish from the temperate Asian distribution type. The genera occupy smaller ranges and are essentially distributed in China and Japan.

These genera can be roughly divided into three subgroups based on their distribution centers in relation to Guizhou. One includes genera extending from the Himalayan region across China to Japan; the other two subgroups have eccentric distribution centers, either westward or northeastward. Members with a westward distribution show a Sino-Himalayan range, from China to the Himalayas; the northeastward group shows a Sino-Japanese pattern, from China to Japan. Among the primarily Eastern Asian genera, about one-fifth belong to the Sino-Himalayan-Japan subgroup, one-fifth to the Sino-Himalayan subgroup, and three-fifths to the Sino-Japanese subgroup. These genera sometimes extend southward into Burma, Indochina, and/or the Malay Archipelago.

Among the genera distributed from the Himalayan region to Japan are: *Choerospondias* B. L. Burtt & A. W. Hill, *Dichocarpum* W. T. Wang & Hsiao, *Hovenia* Thunberg, *Neillia* D. Don, *Houttuynia* Thunberg, *Euscaphis* Siebold & Zuccarini, *Pterostyrax* Siebold & Zuccarini, *Liriope* Loureiro, *Boenninghausenia* Reichenbach ex Meisner, and *Helwingia* Willdenow.

Of the 93 genera in this category in the flora of Fanjing Shan (14.6% of the total genera), 47 are herbaceous, 38 are woody, and 8 are lianoid. The woody genera, such as *Cercidiphyllum* Siebold & Zuccarini, *Acanthopanax* (Decaisne & Planchon) Miquel, *Dendrobenthamia* Hutchinson (= *Cornus* L. subg. *Syncarpea* (Nakai) Q. Y. Xiang), *Enkianthus* Loureiro, *Idesia* Maximowicz, *Platycarya* Siebold & Zuccarini, *Pterocarya* Kunth, and *Tetracentron* Oliver, are important constituents of the broad-leaved forests, while the herbaceous genera, such as *Ophiopogon* Ker-Gawler, *Liriope*, *Reineckea* Kunth, *Tripterospermum* Blume, and *Ainsliaea* DC., play an important role in the herb layer of the same forests. *Sinarundinaria* Nakai is the main constituent under trees in the broad-leaved deciduous forests and in subalpine scrublands.

14. Endemic genera

For the Fanjing Shan mountain range as a whole, 23 of the 636 native genera (3.6%) are endemic to China, but all of them are shared with other provinces. These endemic genera are listed with their ranges and number of species in Table 3. Twelve of these genera are monotypic and nine are oligotypic; the two remaining genera have multiple species. Among the 23 are 11 arborescent genera, of which nine are deciduous and two are evergreen. Eleven genera are herbaceous and only one, *Clematoclethra* Maxim., is lianoid. Except for three genera, *Eurycorymbus* Handel-Mazzetti (Sapindaceae: 1 species), *Dysosma* Woodson (Berberidaceae: 7 species), and *Cunninghamia* R. Brown (Taxodiaceae: 2 species), which occur in Taiwan, all are restricted to central and southeastern China.

Based on the figures cited above we were able to conclude that among the native genera in the flora of Fanjing Shan, 268 (42.1%) are tropical,

TABLE 3. Chinese endemic or near endemic genera in the flora of Fanjing Shan with overall distribution of the genus. The second column indicates the number of species in Fanjing shan/number of species in China.

Asteropyrum (Ranunculaceae)	1/2	Guangxi, Guizhou, Hubei, Hunan, Sichuan, Yunnan.
Bretschneidera (Bretschneideraceae)	1/1	Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, Sichuan, Taiwan, E Yunnan, Zhejiang.
Bostrychanthera (Lamiaceae)	1/1	Fujian, Guangdong, Guangxi, Guizhou, Hubei, Sichuan, Taiwan.
Chimonanthus (Calycanthaceae)	1/2	Anhui, Fujian, Gansu, Guangxi, Guizhou, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Sichuan.
Camptotheca (Nyssaceae)	1/1	Fujian, Hubei, Hunan, Guangdong, Guangxi, Guizhou, Jiangxi, Sichuan.
Clematoclethera (Actinidiaceae)	1/4	Guizhou, Hubei, Shaanxi, Sichuan, Yunnan
Cyclocarya (Juglandaceae)	1/1	Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan, Zhejiang.
Cunninghamia (Taxodiaceae)	1/2	South of the Qinling range.
Davidia (Nyssasaceae)	1/1	Guizhou, Hubei, Sichuan, N Yunnan.
Dysosma (Berberidaceae)	3/7	South of the Qinling range.
Dickinsia (Apiaceae)	1/1	Guizhou, Hubei, Hunan, Sichuan, Yunnan.
Dipteronia (Aceraceae)	1/2	S Gansu, Guizhou, Henan, W Hubei, Shaanxi, Sichuan, SE Yunnan.
Eucommia (Eucommiaceae)	1/1	E to SW China.
Eomecon (Papaveraceae)	1/1	Fujian, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan.
Emmenopterys (Rubiaceae)	1/1	E to SW China (and India).
Eurycorymbus (Sapindaceae)	1/1	S and SW China, Taiwan.
Hanceola (Lamiaceae)	1/8	Guangxi, Guizhou, Hunan, Sichuan, Yunnan.
Latouchea (Gentianaceae)	1/1	Fujian, Guangdong, Guizhou.
Pteroceltis (Ulmaceae)	1/1	N to S and SW China.
Rostrinucula (Lamiaceae)	1/2	Guangxi, Guizhou, Hubei, Hunan, Shaanxi, Sichuan, Yunnan.
Sinojohnstonia (Boraginaceae)	1/3	Guizhou, Hubei, Jiangxi, Shaanxi, Sichuan, Zhejiang.
Thyrocarpus (Boraginaceae)	1/3	Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hubei, S Jiangsu, Jiangxi, E Yunnan.
Whytockia (Gesneriaceae)	1/3	Guizhou, Taiwan, SE Yunnan.

289 (45.4%) are temperate, and 23 (3.6%) are Chinese endemic genera. It is clear in the numbers and percentages that tropical and temperate genera are of about equal importance in the flora of Fanjing Shan. Taking a more general view, however, and looking for ultimate sources, it appears that the flora of Fanjing Shan can be thought of as comprising two main elements, a northern and a southern one, disbursed, as would be expected, along an altitudinal gradient in five vegetational zones (as discussed above).

B. RELATIONSHIPS WITH OTHER MOUNTAINOUS REGIONS IN CHINA

To determine the area's floristic affinities within China, eight mountainous regions in the central and south-central part of the country (Fig. 2) were selected for comparison with the Fanjing Shan region. Based on the worldwide distribution of the genera in the nine mountain regions, 15 distribution patterns can be recognized (Table 4). As expected, temperate genera increase and tropical genera decrease in numbers with increasing latitude. Fanjing Shan, with 268 tropical and 289 temperate genera (excluding the Chinese endemic genera), has about an equal representation of temperate and tropical elements. Taibai Shan, located to the north of Fanjing Shan in Shaanxi province, has 397 (68.0%) temperate and 105 (18.0%) tropical genera; cosmopolitan genera (60, or 10.2%) and endemic genera (22, or 3.8%) make up the remaining 14%. Wuzhi Shan has the highest proportion of tropical genera (88.8%) of any of the areas examined, which would be expected from its southerly location on Hainan Island at about 19°N latitude. The numbers of shared genera and the coefficients of similarity between these mountainous regions are given in Table 5. The higher coefficients of similarity between the Fanjing Shan region (A) and Wuyi Shan (B) (52.8%), the Fanjing Shan region and Shennongjia (D) (50.6%), and the Fanjing Shan region and Jinfo Shan (C) (50.7%) indicate closer phytogeographical links between those four areas

TABLE 4. The principal distribution types of the genera in the floras of nine mountain regions of China. CA = central Asia; COS = cosmopolitan; EA = eastern Asia; EN = endemic; ENA = eastern Asia–North America; MWC = Mediterranean–western and central Asia; NT = North Temperate; OT = Old World tropical; OTE = Old World temperate; PAN = pantropical; TA temperate Asia; TAA = tropical Asia and tropical America; TAF = Tropical Asia and tropical Africa; TAU = tropical Asia and tropical Australia; TSE = tropical Southeast Asia.

Mountain region	Tropical genera								Temperate genera									Total all genera	Area km²
	COS	PAN	TAA	OT	TAU	TAF	TSE	Total	NT	ENA	OTE	TA	MWC	CA	EA	Total	EN		
Fanjing Shan	56	109	11	36	29	23	60	268	115	46	32	6	2	—	91	289	23	636	567
Jinfo Shan	44	77	13	18	12	13	41	174	112	44	32	4	1	—	78	271	26	515	280
Miaoer Shan	43	106	11	35	20	13	66	251	60	34	17	3	—	—	66	180	17	491	267
Nanjiabawa	71	140	20	51	40	41	124	416	183	48	55	14	13	7	124	444	24	955	9,400
Shennongjia	61	121	12	28	22	19	40	242	163	64	52	16	5	—	121	421	47	771	3,250
Taibai Shan	60	63	4	10	6	10	12	105	173	45	73	16	5	4	81	397	22	584	2,379
Wuyi Shan	58	140	13	41	31	28	63	316	101	48	29	5	1	—	91	275	16	665	500
Wuzhi Shan	41	215	22	87	82	55	195	656	28	17	7	1	1	—	29	83	6	786	?
Yulongxue Shan	63	87	4	19	10	23	17	160	155	31	55	14	9	5	62	331	16	570	455

TABLE 5. Degree of similarity of nine major mountain regions in China. Number of shared genera/coefficient of similarity.

		A	B	C	D	E	F	G	H	I
A	Fanjing Shan	—								
B	Wuyi Shan	412/52.8	—							
C	Jinfo Shan	350/50.7	309/41.0	—						
D	Shennongjia	435/50.6	418/46.4	368/46.2	—					
E	Miaoer Shan	330/46.9	343/48.2	313/37.0	251/38.5	—				
F	Nanjiabawa	386/35.6	361/31.9	403/33.8	302/29.1	272/25.7	—			
G	Taibai Shan	289/35.2	259/29.7	374/43.5	253/34.8	174/21.8	341/32.0	—		
H	Yulongxue Shan	272/32.9	241/27.0	326/36.4	222/29.8	187/24.2	340/36.2	270/35.2	—	
I	Wuzhi Shan	254/23.6	293/27.7	237/19.5	160/15.4	309/32.9	234/32.9	113/9.8	141/12.6	—

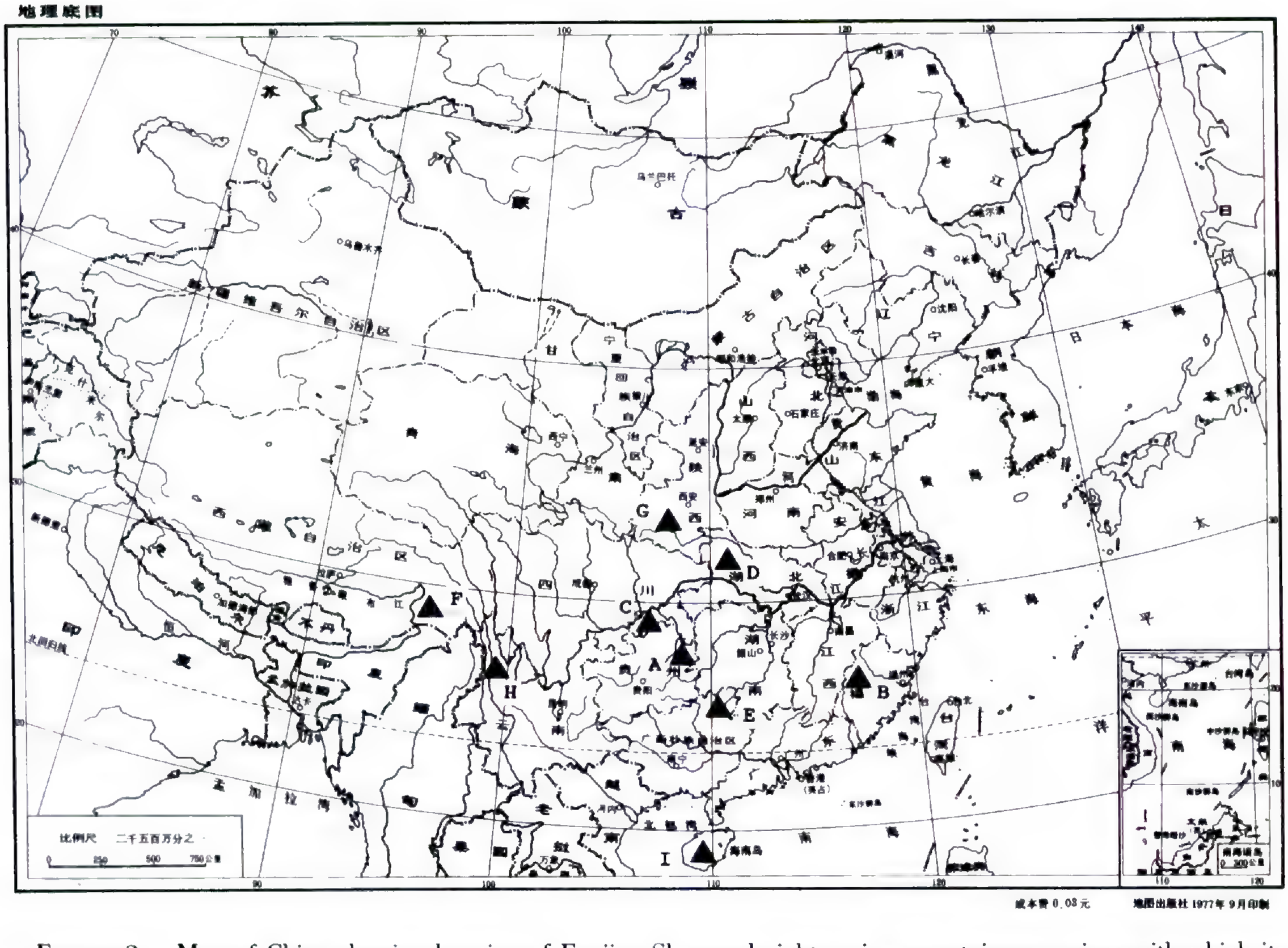

FIGURE 2. Map of China showing location of Fanjing Shan and eight major mountainous regions with which its flora is compared.—A. Fanjing Shan.—B. Wuyi Shan.—C. Jinfo Shan.—D. Shennongjia.—E. Miaoer Shan.—F. Nanjiabawa.—G. Taibai Shan.—H. Yulongxue Shan.—I. Wuzhi Shan.

than between Fanjing Shan and any of the other regions. The significance of the coefficient of similarity between Fanjing Shan and Wuyi Shan on the Fujian-Jiangxi border in eastern China is remarkable because these two ranges are nearly twice as far apart as Fanjing Shan is from either Miaoer Shan (E) in northeastern Guangxi or Jinfo Shan (in southeastern Sichuan), and about 25% farther apart than Fanjing Shan and the Shennongjia region. Noteworthy, however, are the especially low coefficients of similarity between Fanjing Shan and Nanjiabawa (F) in Xizang (Tibet), Taibai Shan (G) in the Qinling Mountains in southern Shaanxi, Yulongxue Shan (H) in northwestern Yunnan and Wuzhi Shan (I) on Hainan, and the clear contrast between regions A to E and regions F to I. The second column in Table 5 shows that the coefficients of similarity between regions B, C, D, and E are still higher than they are with any of the other areas. The coefficients of similarity between I and G (9.8%) and I and H (12.6%) are surprisingly low, attesting to the uniqueness of the Wuzhi Shan flora.

A comparison of the degrees of similarities with nine mountainous regions in China, based on the distribution of genera, shows that the floristic affinities of Fanjing Shan are with Wuyi Shan in southeastern China and secondarily with Jinfo Shan and the Shennongjia region in central China. Phytogeographically, the Fanjing Shan region is transitional between the Sino-Himalayan and Sino-Japanese floras and contains an almost equal number of temperate and tropical genera.

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APPENDIX. Genera in the Fanjing Shan flora and their worldwide distribution. Number of species (approximately): Fanjing Shan/China/worldwide.

1. COSMOPOLITAN	
Amaranthus L.	1/13/40
Anemone L.	3/52/150
Apium L.	1/1/1
Aster L.	2/130/500
Astragalus L.	1/130/2,000
Bidens L.	1/8/230
Carex L.	19/400/1,500–2,000
Clematis L.	10/110/250
Cyperus L.	2/30/550
Digitaria Haller	1/20/380
Eleocharis R. Br.	2/25/200
Eragrostis Wolf	1/35/300
Erigeron L.	1/33/200
Galium L.	1/50/400
Gentiana L.	1/250/500
Geranium L.	2/65/400
Goodyera R. Br.	3/15/40
Hippuris L.	1/1/2–3
Hydrocotyle L.	3/15/75
Hypericum L.	8/55/370
Juncus L.	3/65/300
Lemna L.	1/3/15
Lobelia L.	1/20/250
Lysimachia L.	6/90/200
Mimulus L.	2/5/100
Nymphoides Hill	1/6/20
Oxalis L.	2/10/800
Panicum L.	1/20/500
Physalis L.	1/5/100
Pimpinella L.	2/40/150
Plantago L.	1/16/265
Polygala L.	4/40/500–600
Polygonum L.	12/120/300
Potamogeton L.	1/30/100
Pycreus Pal.	2/10/100
Ranunculus L.	3/90/400
Rhamnus L.	4/59/160
Rorippa Scop.	1/9/70
Rubus L.	26/280/600
Rumex L.	3/30/200
Sagittaria L.	2/6/20
Salvia L.	3/84/700
Sanicula L.	3/22/37
Scirpus L.	1/37/300
Scutellaria L.	1/98/300
Senecio L.	2/160/2,000
Solanum L.	4/39/1,700
Sophora L.	1/23/50
Spirodela Schleiden	1/2/6
Stachys L.	1/18/300
Stellaria L.	1/57/120
Swertia L.	1/50/100
Teucrium L.	2/18/300
Utricularia L.	1/17/120
Viola L.	5/120?/500
Xanthium L.	1/5/30
2. PANTROPICAL GENERA	
Achyranthes L.	3/3/15
Adenostemma Forst. & G. Forst.	1/2/20
Alchornea Sw.	1/6/70
Ardisia Sw.	7/69/400
Aristolochia L.	1/51/300
Arundinella Raddi.	1/11/55
Arundo L.	1/3/12
Bauhinia L.	2/35/300
Begonia L.	2/90/900
Boehmeria Jacq.	8/35/50
Brachiaria Griseb.	1/6/90
Buddleja L.	4/45/100
Bulbophyllum Thouars.	1/36/1,200
Bulbostylis Kunth	1/3/100
Caesalpinia L.	2/16/100
Calanthe R. Br.	4/40/120
Callicarpa L.	5/42/140
Calystegia R. Br.	1/6/25
Cassia L.	2/22/550
Celastrus L.	3/20/35
Celosia L.	1/3/60
Celtis L.	3/20/60
Centipeda Lour.	1/1/6
Cissus L.	1/11/350
Clerodendrum L.	3/30/400
Cocculus DC.	1/2/11
Commelina L.	1/7/100
Conyza Less.	1/8/50
Corchorus L.	1/3/100
Crotalaria L.	6/34/600
Cuscuta L.	2/10/170
Cynanchum L.	4/52/200
Cynodon Rich.	1/2/10
Dalbergia L. f.	2/25/100
Dendropanax Decne. & Planchon	1/16/30
Derris Lour.	1/20/40
Desmodium Desv.	2/55/350
Dioscorea L.	6/49/600
Diospyros L.	5/56/500
Dolichos L.	1/7/70
Eclipta L.	1/1/3–4
Eleusine Gaertner	1/2/10
Erianthus Michaux	1/8/30
Eriocaulon L.	3/45/400
Erythroxylum P. Browne	1/2/250
Euonymus L.	14/90/175
Eupatorium L. s.l.	1/15/1,200
Euphorbia L. s.l.	2/60/2,000
Ficus L.	10/120/800
Fimbristylis Vahl	14/47/200

APPENDIX. Continued.

Gleditsia L.	3/6/16
Glochidion Forst. & G. Forst.	2/25/300
Gouania Jacq.	1/2/20
Haloragis Forst. & G. Forst.	1/2/26
Hibiscus L.	2/24/200
Hypoxis L.	1/1/100
Ilex L.	17/118/400
Impatiens L.	14/190/850
Indigofera L.	3/70/700
Ipomoea L.	1/25/500
Isachne R. Br.	3/15/75
Ischaemum L.	1/15/50
Jasminum L.	1/44/300
Kyllinga Rottb.	1/6/60
Laportea Gaudich.	2/16/23
Lasianthus Jack.	4/32/180
Leersia Sw.	1/4/15
Lindernia All.	3/26/100
Lycianthes Hassler	1/9/200
Mariscus Vahl	1/7/200
Millettia Wight & Arn.	4/30/180
Morinda L.	1/8/80
Murdannia Royle	3/18/50
Nertera Banks & Sol. ex Gaertner	1/1/12
Oplismenus Pal.	1/3/15
Ormosia Jackson	1/35/120
Ottelia Pers.	1/8/40
Paspalum L.	1/10/250
Pennisetum Rich. ex Pers.	1/8/70
Perrottetia Kunth	1/3/20
Phaseolus L.	1/15/50
Phytolacca L.	1/4/35
Pilea Lindley	6/65/400
Piper L.	1/35/2,000
Pouzolzia Gaudich.	1/5/50
Pratia Gaudich.	1/3/35
Psychotria L.	1/15/700
Rapanea Aublet	2/7/200
Sacciolepis Nash	1/3/30
Sapium P. Browne	2/9/120
Schefflera Forst. & G. Forst.	2/37/200
Schoepfia Schreber	1/3/25
Setaria Pal.	4/17/140
Siegesbeckia L.	2/3/6
Smilax L.	11/61/300
Sporobolus R. Br.	1/6/150
Styrax L.	4/55/130
Symplocos Jacq.	11/125/350
Ternstroemia Mutis ex L. f.	1/20/100
Torenia L.	2/11/50
Trema Lour.	2/6/30

APPENDIX. Continued.

Triumfetta L.	1/8/150
Uncaria Schreber	1/13/60
Urena L.	1/4/6
Verbena L.	1/1/250
Vitex L.	1/20/250
Wahlenbergia Schrader ex Roth.	1/1/150
Zanthoxylum L.	5/50/250
Zizyphus Miller	1/13/100

3. TROPICAL AMERICA AND TROPICAL ASIA

Clethra L.	4/16/70
Gaultheria L.	1/26/210
Lindera Thunb.	8/54/100
Litsea Lam.	7/64/400
Meliosma Blume	4/10/25
Microtropis Wallich ex Meissner	2/30/70
Mirabilis L.	1/1/60
Picrasma Blume	1/2/6
Sageretia Brongn.	2/14/35
Sloanea L.	3/14/100
Turpinia Vent.	1/10/30

4. OLD WORLD TROPICS

Alangium Lam.	3/8/17
Albizia Durazz.	2/17/150
Alpinia Roxb.	2/26/250
Asparagus L.	1/24/300
Blumea DC.	1/30/50
Capillipedium Stapf	1/6/10
Cayratia Juss.	3/13/45
Centotheca Desv.	1/1/4
Clausena Burm. f.	1/10/25
Didymocarpus Wallich	1/47/120
Dopatrium Buch.-Ham ex Bentham	1/1/12
Elatostema Forst. & G. Forst.	2/39/200
Embelia Burm. f.	2/20/130
Emilia Cass.	1/4/30
Eulalia Kunth	1/11/30
Euodia Lam.	3/25/45
Galeola Pour.	1/4/25
Gardenia Ellis	1/6/250
Grewia L.	1/27/150
Maesa Forssk.	3/27/200
Mallotus Lour.	4/40/142
Monochoria C. Presl	1/5/6
Mussaenda L.	2/28/200
Osbeckia L.	1/12/100
Pharus P. Browne	1/9/50
Pittosporum Banks ex Gaertner	9/34/150
Pollia Thunb.	1/6/16
Porana Burn. f.	1/14/24
Rostellularia Reichb.	1/3/22

APPENDIX. Continued.

Smithia Aiton	2/4/30
Stephania Lour.	3/30/50
Syzygium Gaertner	1/72/500
Tinospora Miers.	1/7/32
Uraria Desv.	1/9/20
Viscum L.	1/12/100
Zehneria Endl.	1/12/30

5. TROPICAL ASIA AND TROPICAL AUSTRALIA

Aglaia Lour.	1/10/250–300
Ailanthus Desf.	1/5/10
Alyxia R. Br.	1/18/112
Balanophora Forst. & Forst.	3/19/80
Boea Comm. ex Lam.	1/3/17
Cinnamomum Schaeffer	7/46/250
Cleisostoma Blume	1/20/100
Cudrania Trécul.	1/4–8/12
Dendrobium Sw.	2/63/1,400
Dimeria R. Br.	1/4/40
Dunbaria Wight & Arn.	1/7/25
Elaeocarpus L.	2/38/200
Eremochloa Buese.	2/4/10
Eria Lindley	1/36/350
Gastrodia R. Br.	1/3/20
Helicia Lour.	1/18/90
Lagerstroemia L.	2/15/53
Leptopus Decne.	1/8/11
Mazus Lour.	1/22/30
Microcarpaea R. Br.	1/1/1
Nothopanax Miq. emend. Harms	1/3/15
Rabdosia Hassk.	2/77/100
Spathoglottis Blume	1/2/40
Tetrastigma Planchon	3/45/90
Thrixspermum Lour.	1/10/100
Toona M. Roemer	2/3/15
Trichosanthes L.	3/40/55
Wikstroemia Endl.	1/40/70
Zingiber Boehmer	2/14/85

6. TROPICAL ASIA AND TROPICAL AFRICA

Amorphophallus Blume ex Decne.	1/25/100
Arthraxon Pal.	1/6/15
Asystasiella Lindau	1/1/3
Crassocephalum Moench	1/1/30
Debregeasia Gaudich.	2/4/5
Dichrocephala L'Hérit. ex DC.	1/3/10
Dregea E. Meyer	1/5/12
Girardinia Gaudich.	1/7/8
Gynura Cass.	1/15/100
Lecanthus Wedd.	1/3/5
Microstegium Nees	2/10/30
Miscanthus Andersson	1/6/20

APPENDIX. Continued.

Myrsine L.	2/4/7
Neyraudia Hook. f.	1/2/6
Peristrophe Nees	1/5/30
Premna L.	2/45/200
Ricinus L.	1/1/1
Strobilanthes Blume	2/20/250
Taxillus Tieghem	2/15/60
Themeda Forssk.	1/4/10
Thladiantha Bunge	3/29/30
Toddalia Juss.	1/1/1
Tricalysia A. Rich. ex DC.	1/4/100

7. TROPICAL SOUTHEAST ASIA

Adinandra Jack	3/20/80
Aeginetia L.	1/3/10
Aganosma G. Don f.	1/5/15
Aleurites Forst. & G. Forst.	1/1/2
Alniphyllum Matsum.	1/2/2
Altingia Noronha	4/8/12
Amentotaxus Pilger.	1/3/3
Amesiodendron Hu	1/2/2
Brandisia Hook. & Thompson	1/8/11–13
Briggsia Craib.	1/18/20
Broussonetia L'Hérit. ex Vent.	2/5/5
Camellia L.	6/190/220
Campanumoea Blume	2/4/8
Carrierea Franchet	1/2/3
Chirita Buch.-Ham. ex D. Don	1/40/80
Chlamydoboea Stapf	1/2/2
Chloranthus Sw.	3/15/35
Christisonia Gardner	1/1/17
Cipadessa Blume	1/2/3
Coix L.	1/1/5
Collabium Blume	1/2/8
Coptosapelta Korth.	1/1/13
Cyclea Arn. ex Wight	1/13/30
Daphniphyllum Blume	3/10/24
Dichroa Lour.	1/4/13
Distylium Siebold & Zucc.	3/12/18
Engelhardia Leschen. ex Blume	1/6/15
Exbucklandia R. W. Br.	1/2/3
Eurya Thunb.	12/60/130
Gastrochilus D. Don	2/12/22
Globba L.	2/3/70
Gynostemma Blume	1/2/2
Hemiboea C. B. Clarke	4/5/8
Hemsleya Cogn.	2/2/2
Indocalamus Nakai	1/17/20
Kadsura Juss.	1/7/22

APPENDIX. Continued.

Lysidice Hance	1/2/2
Machilus Nees	7/68/100
Manglietia Blume	1/19/32
Michelia L.	2/35/55
Myrioneuron R. Br. ex Kurz.	1/4/15
Neolitsea Merr.	4/40/80
Oenanthe L.	3/11/30
Ophiorrhiza L.	2/25/150
Oreocnide Miq.	1/9/20
Paederia L.	2/11/50
Pellionia Gaudich.	1/16/50
Phoebe Nees	4/34/70
Phyllagathis Blume	1/28/35
Pleione D. Don	1/10/10
Pueraria DC.	1/9/20
Reevesia Lindsey	1/14/18
Sabia Colebr.	1/10/19
Sarcandra Gardner	1/2/3
Sarcococca Lindley	1/8/20
Sarcopyramis Wallich	1/1/1
Schima Reinw. ex Blume	3/9/15
Sindechites Oliver	1/2/3
Sycopsis Oliver	1/2/7
Ypsilandra Franchet	1/4/5
8. NORTH TEMPERATE	
Abies Miller	1/18/50
Acer L.	12/100/200
Aconitum L.	3/160/300
Acorus L.	1/3/3
Actaea L.	1/2/10
Adenocaulon Hook.	1/1/5
Aesculus L.	1/8/13
Agrimonia L.	1/4/15–20
Alisma L.	1/3/10
Allium L.	1/110/700
Alnus Miller	2/8/40
Anaphalis DC.	3/50/100
Androsace L.	1/60/100
Angelica L.	3/26/80
Aquilegia L.	1/9/100
Arenaria L.	1/60/250
Arisaema C. Martius	5/82/150
Artemisia L.	6/170/350
Asarum L.	3/30/70
Berberis L.	7/160/450
Betula L.	3/29/100
Buxus L.	3/11/70
Capsella Medikus	1/1/5
Carpinus L.	8/24/45
Castanea Miller	4/4/12
Cephalanthera Rich.	1/6/14
Cerastium L.	1/22/60
Cercis L.	1/5/7
Chrysosplenium L.	1/42/55

APPENDIX. Continued.

Cimicifuga Wernisch.	1/8/15
Circaea L.	4/7/8
Cirsium Miller	3/50/200
Clinopodium L.	3/11/20
Coptis Salisb.	1/6/15
Coriaria L.	1/3/15
Cornus L.	5/22/45
Corydalis DC.	1/200/320
Corylus L.	2/7/15
Cotoneaster Medikus	5/45/50
Cryptotaenia DC.	1/1/5
Cupressus L.	1/5/13
Cynoglossum L.	2/10/50–60
Cypripedium L.	1/23/40
Deutzia Thunb.	1/40/50–60
Deyeuxia Clarion ex Pal.	3/43/100
Elaeagnus L.	5/10/45
Epilobium L.	8/37/165
Fagus L.	3/5/10
Fraxinus L.	2/25/70
Habenaria Willd.	1/70/500
Halenia Borkh.	1/2/103
Heracleum L.	1/23/60
Iris L.	1/40/300
Juglans L.	1/4/15–20
Leontopodium R. Br.	1/41/50
Ligusticum L.	1/30/60
Lilium L.	2/40/80
Listera R. Br.	7/18/30
Lonicera L.	6/100/180
Malus Miller	4/22/25
Malva L.	3/4/40
Melandrium Röhl.	1/33/100
Mentha L.	1/6/25
Monotropa L.	1/1/5
Morus L.	3/6/10
Myrica L.	1/4/50
Orobanche L.	1/25/150
Ostrya Scop.	1/4/10
Oxytropis DC.	1/30/300
Parnassia L.	1/36/50
Pedicularis L.	5/350/600
Philadelphus L.	1/15/65
Pinus L.	2/22/95
Platanthera Rich.	2/40/200
Polygonatum Miller	2/35/55
Populus L.	1/25/35
Potentilla L.	4/90/500
Primula L.	2/300/500
Prunella L.	1/3/7
Prunus L.	17/140/200
Pyrola L.	2/23/25
Quercus L.	14/70/450
Rhodiola L.	2/75/90
Rhododendron L.	16/650/800

APPENDIX. Continued.

Rhus L.	3/6/250
Ribes L.	3/45/150
Rosa L.	2/82/200
Rubia L.	2/17/60
Sabina Miller	1/14/50
Sagina L.	1/4/30
Salix L.	10/200/500
Sambucus L.	2/5/20
Saussurea DC.	5/320/403
Saxifraga L.	1/180/370
Sedum L.	4/125/350
Solidago L.	1/1/100
Sorbus L.	8/55/85
Spiraea L.	6/50/100
Spiranthes Rich.	1/2/40
Streptopus Michaux	1/5/10
Thalictrum L.	5/67/150
Tilia L.	1/35/50–80
Trifolium L.	1/7/300
Ulmus L.	1/23/45
Urtica L.	1/15/50
Vaccinium L.	5/47/450
Valeriana L.	4/24/200
Veratrum L.	1/13/25
Veronica L.	1/64/250
Viburnum L.	11/74/150
Vicia L.	1/40/150
Vitis L.	7/25/60–70

9. EASTERN ASIA AND NORTH AMERICA

Abelia R. Br.	2/6/30
Aletris L.	1/13/25
Ampelopsis Michaux	1/1/2
Amphicarpaea Elliot ex Nutt.	1/1/3
Antenoron Raf.	2/2/4
Apios Fabr.	1/6/10
Aralia L.	3/30/35–40
Astilbe Buch.-Ham ex D. Don	1/15/25
Berchemia Necker ex DC.	2/16/22
Cacalia L.	1/50/80
Castanopsis Spach.	7/60/122
Caulophyllum Michaux	1/1/3
Cladrastis Raf.	1/5/6
Cleyera Thunb.	3/11/17
Disporum Salisb. ex D. Don	3/10/20
Hamamelis L.	1/2/6
Hugeria Small	1/2/3
Hydrangea L.	15/45/80
Illicium L.	1/21/42
Itea L.	1/12/15
Leibnitzia Cass.	1/3/7
Lespedeza Michaux	4/25/40
Liquidambar L.	2/2/5

APPENDIX. Continued.

Liriodendron L.	1/1/2
Lithocarpus Blume	9/70/300
Lyonia Nutt.	3/6/35
Magnolia L.	4/30/90
Mahonia Nutt.	4/40/80
Meehania Britton	3/5/7
Muhlenbergia Schreber	2/6/100
Nyssa L.	1/6/10
Osmanthus Lour.	2/15/17
Panax L.	1/6/8
Parthenocissus Planchon	4/9/15
Photinia Lindley	4/40/60
Phryma L.	1/1/1
Pieris D. Don	1/6/10
Pogonia Juss.	1/3/10
Sassafras Nees & Eberm.	1/2/3
Schisandra Michaux	1/19/25
Smilacina Desf.	1/18/30
Tiarella L.	1/1/5
Toxicodendron Miller	3/15/20
Trachelospermum Lemaire	6/10/20
Tsuga Carrière	3/5/14
Veronicastrum Moench	1/14/20

10. OLD WORLD TEMPERATE

Adenophora Fischer	2/49/60
Ajuga L.	1/18/40–50
Anthriscus Pers.	1/2/20
Asyneuma Griseb. & Schenk.	1/1/51
Carpesium L.	4/10/20
Cucubalus L.	1/1/1
Daphne L.	2/35/70
Dendranthema Des Moul.	1/17/30
Dipsacus L.	2/8/15
Elsholtzia Willd.	4/33/35
Epimedium L.	2/14/21
Fagopyrum Miller	2/8/15
Hemerocallis L.	1/11/15
Inula L.	1/20/200
Lactuca L.	1/40/118
Leontice L.	1/2/3–5
Ligularia Cass.	3/100/150
Ligustrum L.	5/38/51
Lotus L.	1/3/100
Melissa L.	1/3/4
Nerium L.	1/2/4
Origanum L.	1/1/15–20
Paris L.	3/16/20
Peucedanum L. (also Africa)	2/30/170
Phlomis L.	1/43/100
Pyracantha M. Roemer	3/7/10

APPENDIX. Continued.

Roegneria K. Koch	1/70/90
Scopolia Jacq.	1/2/5
Tamarix L.	1/18/60
Torilis Adan.	1/2/12
Zelkova Spach	2/4/6–7
11. TEMPERATE ASIA	
Bergenia Moench	1/6/10
Campylotropis Bunge	1/50/65
Kalimeris Cass.	1/7/20
Myriactis Less.	2/5/10
Trigonotis Steven	2/32/50
Tripterospermum Blume	6/20/35
12. MEDITERRANEAN, WESTERN TO CENTRAL ASIA, AND NORTH TO CENTRAL ASIA	
Pistacia L.	1/2/10
13. EASTERN ASIA	
Acanthopanax Miq.	7/27/35
Actinidia Lindley	4/52/54
Ainsliaea DC.	2/45/70
Akebia Decne.	2/2/5
Amitostigma Schltr.	1/20/23
Aucuba Thunb.	1/3/4
Aulacolepis Hacket	1/2/4
Beesia Balf. f. & W. W. Sm.	1/2/2
Belamcanda Adanson	1/1/2
Bletilla Reichb. f.	1/4/6
Bothrispermum Bunge	1/5/5
Cardiocrinum Lindley	2/2/3
Caryopteris Bunge	1/12/15
Catenaria Bentham	1/1/1
Cephalotaxus Sieb. & Zucc.	3/7/9
Cercidiphyllum Sieb. & Zucc.	1/1/1
Choerospondias B. L. Burtt & A. W. Hill	1/1/1
Codonopsis Wallich	2/39/50
Corylopsis Sieb. & Zucc.	5/20/30
Cremastra Lindley	1/2/7
Decaisnea Hook. & Thomson	1/1/1
Deinostema Yamazaki	1/1/2
Dendrobenthamia Hutch.	2/12/12
Dichocarpum W. T. Wang & Hsiao	1/9/18
Disporopsis Hance	1/4/4
Enkianthus Lour.	3/7/10
Euscaphis Sieb. & Zucc.	1/1/1
Gardneria Wallich	1/5/6

APPENDIX. Continued.

Ginkgo L.	1/1/1
Helwingia Willd.	2/4/4
Hemiphragma Wallich	1/1/1
Holboellia Wallich	2/11/12
Hosta Tratt.	1/3/40
Houttuynia Thunb.	1/1/1
Hovenia Thunb.	1/3/3
Idesia Maxim.	1/1/1
Kalopanax Miq.	1/1/1
Kerria DC.	1/1/1
Keteleeria Carrière	1/2/2
Kummerowia Schindler	1/2/2
Liriope Lour.	2/6/8
Loropetalum R. Br. ex Reichb.	1/2/3
Lycoris Herbert	2/15/20
Lysionotus D. Don	1/29/31
Macleaya R. Br.	1/2/2
Maddenia Hook. & Thomson	2/4/5
Mosla Buch.-Ham. ex Maxim.	3/11/22
Nandina Thunb.	1/1/1
Nonocnide Blume	1/2/4
Neillia D. Don	1/10/12
Nothosmyrnium Miq.	1/2/2
Ophiopogon Ker-Gawler	7/40/60
Oreocharis Bentham	2/20/20
Patrinia Juss.	3/13/20
Paulownia Sieb. & Zucc.	2/6/17
Perilla L.	1/1/1
Phtheirospermum Fisch. & Meyer	2/3/7
Phyllostachys Sieb. & Zucc.	3/40/50
Pileostegia Hook. & Thomson	1/2/3
Platycarya Sieb. & Zucc.	2/2/2
Pogonatherum Pal.	1/2/2
Prinsepia Royle	1/4/4
Pternopetalum Franchet	3/25/27
Pterocarya Kunth	1/9/10
Pterostyrax Sieb. & Zucc.	2/2/4
Reineckea Kunth	1/1/1
Rhaphiolepis Lindley	1/7/14
Rhynchospermum Reinw.	1/1/2
Rohdea Roth	1/1/1
Sargentodoxa Rehd. & Wils.	1/1/1
Schizophragma Sieb. & Zucc.	3/6/8
Semiaquilegia Makino	1/1/7

APPENDIX. Continued.

Serissa Comm. ex Juss.	1/2/3
Sinarundinaria Nakai	2/10/23
Sinomenium Diels	1/1/1
Siphocranion Kudo	2/2/2
Siphonostegia Bentham	2/2/3
Spatholirion Ridley	1/3/3
Spodiopogon Trin.	1/6/10
Stachyurus Sieb. & Zucc.	4/8/10
Stauntonia DC.	4/22/25
Stranvaesia Lindley	1/4/5
Tetracentron Oliver	1/1/1
Toricellia DC.	1/2/3
Tricyrtis Wallich	1/5/11
Triplostegia Wallich ex DC.	1/2/2
Tripterygium Hook. f.	1/4/4
Tubocapsicum Makino	1/2/2
Tupistra Ker-Gawler	2/16/25
Weigela Thunb.	1/4/12
Youngia Cass.	1/40/50
14. ENDEMIC TO CHINA	
Asteropyrum J. R. Drumm. & Hutch.	1/2
Bostrychanthera Bentham	1/2
Bretschneidera Hemsley	1/1
Camptotheca Decne.	1/1
Chimonanthus Lindley	1/3
Clematoclethra Maxim.	1/1
Cunninghamia R. Br.	1/2
Cyclocarya Iljinsk.	1/1
Davidia Baillon	1/1
Dickinsia Franchet	1/1
Dipteronia Oliver	1/2
Dysosma Woodson	3/7
Emmenopterys Oliver	1/1
Eomecon Hance	1/1
Eucommia Oliver	1/1
Eurycorymbus Hand.-Mazz.	1/1
Hanceola Kudo	1/8
Latouchea Franchet	1/1
Pteroceltis Maxim.	1/1
Rostrinucula Kudo	1/2
Sinojohnstonia Hu	1/2
Thyrocarpus Hance	1/3
Whytockia W. W. Sm.	1/2

REVISION DEL GENERO *STREPTOSTACHYS* (POACEAE–PANICOIDEAE), SU POSICION SISTEMATICA DENTRO DE LA TRIBU PANICEAE[1]

Osvaldo Morrone[2] *and Fernando Zuloaga*[2]

Resumen

Los límites genéricos de *Streptostachys* Desv. son discutidos, tomando en consideración caracteres exomorfológicos y anatómicos. *Streptostachys* queda principalmente definido por poseer raquilla engrosada entre la gluma inferior y el antecio superior, cariopsis con hilo linear, antecio superior papiloso y piloso y lígula ciliada o ausente. Se consideran dentro del género a *S. asperifolia*, *S. macrantha*, y *S. ramosa*. *Streptostachys acuminata* es tratada como *Urochloa acuminata* y *S. robusta* como una especie dudosa dentro del género *Ichnanthus*.

Abstract

In this work the generic limits of *Streptostachys* Desv. are discussed, considering exomorphological and anatomical characters. *Streptostachys* is mainly defined here by the thickening of the rachilla, caryopsis with a linear hilum, ornamentation of the upper anthecium and with the ligule ciliate or absent. Three species are treated within the boundaries of *Streptostachys*: *S. asperifolia*, *S. macrantha*, and *S. ramosa*. *Streptostachys acuminata* is treated as *Urochloa acuminata* and *S. robusta* is discussed and considered as a doubtful species of *Ichnanthus*.

El género *Streptostachys* fue creado por Desvaux en el año 1810 sobre la base de una especie, *S. asperifolia* Desv.

Streptostachys fue estudiado por varios autores en los últimos años, incluyendo el análisis del género en particular o como parte de floras regionales o de estudios de géneros de gramíneas para todo el mundo.

Renvoize (1984b) incluyó dentro de *Streptostachys* cinco especies en su tratamiento de las gramíneas de Bahia y lo caracterizó por incluir plantas anuales o perennes, con espiguillas solitarias o apareadas sobre inflorescencias racemosas, gluma inferior ⅓ a ¾ del largo de la espiguilla y separada de la gluma superior por un entrenudo corto.

Zuloaga & Soderstrom (1985) trataron en *Streptostachys* a *S. asperifolia*, *S. macrantha* (Trin.) Zuloaga & Soderstrom, y *S. ramosa* Zuloaga & Soderstrom por tener lígulas ciliadas o ausentes, espiguillas engrosadas entre la gluma inferior y el antecio superior, cariopsis con hilo linear y antecio superior piloso y con papilas simples distribuidas regularmente en toda la superficie.

Clayton & Renvoize (1986) consideraron a *Streptostachys* como género monotípico, ubicando a *S. ramosa* y *S. macrantha* en *Panicum*, no validando en el primer caso la combinación correspondiente, y sin mencionar las especies descriptas por Renvoize en 1984a, *S. robusta* y *S. acuminata*. Estos autores distinguieron al género básicamente por poseer raquilla engrosada e incurva por debajo de la inserción de la espiguilla; citaron la presencia de células fusoides en el género y lo relacionaron con *Acroceras* por poseer hilo linear.

Watson & Dallwitz (1988) siguieron el criterio

[1] Deseamos expresar nuestra gratitud al Gerrit Davidse por la revisión crítica del manuscrito, su valioso aporte acerca de la presencia de eleosoma en *S. asperifolia*, y sus opiniones sobre la delimitación del género y especies dentro del mismo.

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de Clayton & Renvoize (1986), sin discutir las relaciones de *Streptostachys* ni mencionar la ubicación de las especies excluidas del mismo. Watson & Dallwitz describieron al género con lígulas ciliadas o ausentes, espiguillas comprimidas dorsiventralmente, con raquilla conspicua entre la gluma inferior y superior y entre la flor inferior y superior, antecio superior estipitado, glumas subiguales, flor inferior con o sin pálea y masculina o neutra; antecio superior endurecido y cariopsis con hilo linear. Anatómicamente caracterizaron a *Streptostachys* como no-Kranz y con células fusoides.

Todos los autores previamente citados no han tomado en consideración la totalidad de las especies descriptas dentro del género para su delimitación en la tribu Paniceae, ni han analizado los caracteres exomorfológicos y anatómicos de las mismas.

En el presente trabajo se estudian las entidades hasta ahora incluidas en *Streptostachys* desde el punto de vista exomorfológico e histofoliar, aportándose nuevos datos y discutiéndose la delimitación de *Streptostachys* y su ubicación taxonómica dentro de la tribu Paniceae.

Materiales y Metodos

El estudio exomorfológico fue realizado sobre la base de materiales de los siguientes herbarios: BAA, CEN, CEPEC, F, G, IAN, IBGE, K, M, MO, NY, P, R, RB, SI, SP, UB, US, y W.

Las fotografías de cortes transversales de hoja y epidermis fueron tomadas con un microscopio electrónico de barrido, siendo el aparato utilizado un *Jeol* JSM-25 SII, de la Facultad de Odontología (Universidad Nacional de Buenos Aires, Argentina).

Para el estudio de los caracteres histofoliares se empleó la penúltima lámina de la innovación fértil, realizándose los cortes transversales y longitudinales en el tercio medio de la lámina. Se utilizó material proveniente de ejemplares de herbario, previo tratamiento con Contrad 70 (Schmid & Turner, 1977). Para la obtención de ambas epidermis se siguió el método de Metcalfe (1960).

Los cortes fueron realizados a mano alzada y coloreados con azul de metileno al 1% en agua, y safranina al 1% en alcohol 80° o con safranina-fast green y montados en gelatina-glicerina o en bálsamo de Canadá. Para la observación de las células clorenquimáticas se realizaron macerados siguiendo el método de Jeffrey (Sass, 1940). Para la identificación de los cuerpos de sílice y células suberosas se utilizó respectivamente fenol (Metcalfe, 1960) y Sudán III (Sass, 1940). Para la detección de cristales se siguió el método propuesto por Sánchez & Casabona (1981). La determinación de almidón y su distribución se realizó mediante unas gotas de solución iodo-iodurada (Sass, 1940).

La presencia de aceites en la espiguilla se detectó con el reactivo Sudán IV (Jensen, 1962). Para la caracterización de lignina se utilizó floroglucina clorhídrica (Johansen, 1940). Las observaciones y dibujos fueron realizados con un microscopio Wild M20 con cámara de dibujo. Para las descripciones se adoptó la terminologiá propuesta por Ellis (1976, 1979). Los ejemplares utilizados para el estudio histofoliar de las especies han sido identificados con un * en la cita del material examinado.

Resultados y Discusion

De acuerdo con los resultados obtenidos en el presente trabajo se ha hallado una manifiesta variabilidad en las cinco especies revisadas. Consecuentemente, se han tratado de establecer caracteres válidos para definir el género y cuales son las especies que pertenecen al mismo.

Así, se considera que el poseer lígula ciliada o ausente; espiguilla comprimida dorsiventralmente, con raquilla engrosada y manifiesta entre las glumas, antecio inferior y superior; antecio superior piloso y papiloso, y cariopsis con hilo linear, ocupando todo el largo de la cariopsis, son los caracteres que permiten distinguir a *Streptostachys* del resto de los géneros afines pertenecientes a la tribu Paniceae.

RAQUILLA

Zuloaga & Soderstrom (1985), Clayton & Renvoize (1986), y Watson & Dallwitz (1988), mencionaron entre los caracteres distintivos de *Streptostachys* la presencia de raquilla engrosada. Este engrosamiento se encuentra tanto en *S. asperifolia* como en *S. macrantha* y *S. ramosa*; en las tres especies la raquilla se halla conspicuamente endurecida y ensanchada entre la gluma inferior y el antecio superior, siendo los bordes inferiores involutos en *S. asperifolia* y rectos en *S. macrantha* y *S. ramosa*. Al efectuar cortes transversales de la raquilla en *S. asperifolia* se observó que la misma es hueca en la porción distal debajo del antecio superior, mientras que en *S. macrantha* y *S. ramosa* la raquilla se presenta maciza en toda su extensión a la madurez de la espiguilla (Fig. 1D).

Se ha detectado un eleosoma en la porción engrosada de la raquilla en espiguillas maduras de *S. asperifolia*, *S. macrantha*, y *S. ramosa*. A través de un ensayo con Sudán IV se hallaron abundantes

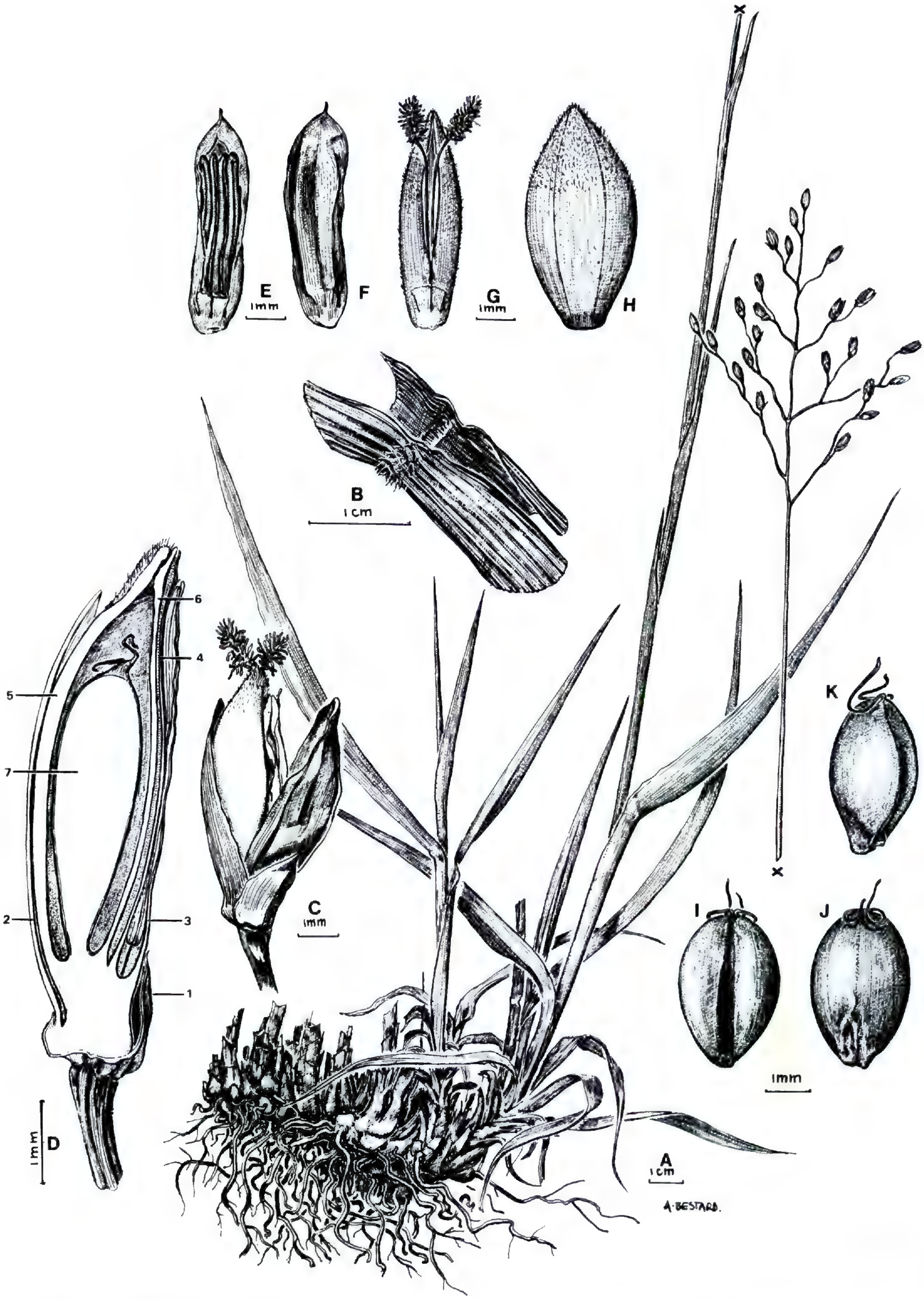

FIGURA 1. *Streptostachys macrantha.*—A. Aspecto general.—B. Detalle de la región ligular.—C. Espiguilla, vista lateral.—D. Corte longitudinal de espiguilla: 1, gluma inferior; 2, gluma superior; 3, lemma inferior; 4, pálea inferior; 5, lemma superior; 6, pálea superior; 7, cariopsis.—E. Flor inferior con estambres y lodículas.—F. Pálea inferior.—G. Pálea superior con lodículas.—H. Antecio superior, vista ventral.—I. Cariopsis, vista hilar.—J. Cariopsis, vista escutelar.—K. Cariopsis, vista lateral. (De *Irwin & Soderstrom 7131.*)

gotitas de aceite en la epidermis y tejidos hipodérmicos de la raquilla, principalmente entre la inserción de la gluma inferior y superior.

La presencia de este tejido en diásporas de gramíneas ha sido extensamente correlacionada con la dispersión a través de hormigas (mirmecofilia), habiendo sido documentada la existencia de eleosoma en diversos géneros de gramíneas (Davidse, 1987). Beattie (1983) señaló diversas hipótesis para el establecimiento de la mirmecofilia, entre las que incluye protección contra el fuego, dispersión a distancia, y el hecho de poseer los hormigueros un microhabitat rico en nutrientes.

HILO

Si bien no existen estudios generales sobre el tipo de hilo y sus relaciones evolutivas en las gramíneas, en particular en la tribu Paniceae, Filgueiras (1986) y Sendulsky et al. (1987) consideraron la utilización del mismo de valor taxonómico.

Clayton & Renvoize (1986) citaron hilo linear en la tribu Paniceae en los géneros *Acroceras* Stapf, *Homolepis* Chase, *Louisiella* Hubbard & Leonard, *Mesosetum* Steudel, *Oplismenopsis* Parodi, *Streptostachys*, *Tatianyx* Zuloaga & Soderstrom y en cinco especies de *Panicum*.

En la presente revisión se considera importante el carácter de hilo linear para la delimitación de géneros dentro de las Paníceas, y se desestima el considerar a *Panicum* como un género variable en lo que a este carácter se refiere. Así, de las cinco especies citadas por Clayton & Renvoize (1986) para el género, las tratadas como *Panicum ramosum* y *Panicum macranthum* pertenecen al género *Streptostachys*, *Panicum glutinosum* Sw., y *Panicum villaricense* Mez a *Homolepis* (Zuloaga & Soderstrom, 1985).

La restante especie con hilo linear tratado por Clayton & Renvoize (1986) en *Panicum*, *P. pilgerianum* (Schweick.) Clayton, originalmente descripta para el género *Acroceras*, fue segregada por Launert (1970) en el género *Psilochloa*, caracterizándose el género por ser Kranz, del subtipo anatómico PS y con hilo linear.

TIPO DE LÍGULA Y ORNAMENTACIÓN DEL ANTECIO SUPERIOR

Webster (1988), en su tratamiento de los géneros de Paníceas de América del Norte, consideró entre los caracteres genéricos distintivos en la tribu el tipo de lígula, la presencia o ausencia de la misma, y la ornamentación y textura del antecio superior. La lígula es ciliada a nula en *S. asperifolia*, *S. macrantha*, y *S. ramosa*, mientras que el antecio superior se presenta endurecido y piloso con papilas simples distribuidas regularmente en toda su superficie.

ANATOMÍA FOLIAR

Los caracteres epidérmicos de las especies analizadas responden al dermotipo panicoide, el que se caracteriza por poseer micropelos bicelulares fusiformes, cuerpos de sílice costales halteriformes o menos frecuentemente nodulares, aparatos estomáticos romboidales a subdiscoidales, y células cortas solitarias o en pares en la zona intercostal (Metcalfe, 1960; Prat, 1932, 1936; Tateoka et al., 1959).

El estudio de los caracteres histofoliares de *S. asperifolia*, *S. macrantha*, y *S. ramosa* ha permitido observar discrepancias en lo que al síndrome de Kranz se refiere.

De acuerdo con los caracteres histofoliares *S. macrantha* y *S. ramosa* son dos especies Kranz, del subtipo anatómico MS por tener:

—Presencia de una vaina mestomática Kranz alrededor de los haces vasculares, cuyas células poseen cloroplastos especializados.
—Ausencia de vaina parenquimática.
—Presencia de almidón en la vaina Kranz.
—Cuatro tipos de haces vasculares, con haces vasculares de tercer y cuarto orden por debajo de las células buliformes.
—Dos a tres células clorenquimáticas entre haces vasculares contíguos.
—Células Kranz rectangulares, alargadas longitudinalmente en vista paradermal.
—Relación de isótopos estables del carbono ($\delta^{13}C$). R. H. Brown (comm. pers.) reportó un $\delta^{13}C$ de − 14.39‰ y 12.19‰ para *S. macrantha* y *S. ramosa* respectivamente.

Hattersley & Watson (1976) establecieron un carácter para diferenciar los distintos subtipos fisiológicos presentes en gramíneas, distinguiendo el tipo XYMS-, el cual se corresponde con el subtipo MS de Brown (1977) y Ellis (1977) por presentar las células Kranz en contacto directo con los elementos del metaxilema. Se ha observado que este carácter es variable tanto en *S. macrantha* como en *S. ramosa*, hallándose, aún dentro de un mismo ejemplar, haces vasculares primarios con o sin células intermedias entre la vaina Kranz y los elementos de metaxilema.

Streptostachys asperifolia es, en cambio, una especie no-Kranz, con doce células clorenquimá-

ticas entre haces vasculares contíguos, presencia de almidón en las células clorenquimáticas, haces vasculares con vaina mestomática y parenquimática sin cloroplastos especializados, hallándose en la especie células fusoides y mesófilo laxo. Brown (1977) reportó para esta especie un valor de isótopos estables del carbono de −27.0‰.

El hecho de poseer *S. asperifolia* un tipo fotosintético y anatómico diferente al presente en *S. macrantha* y *S. ramosa*, podría implicar la exclusión de las dos últimas especies de *Streptostachys*. Existen sin embargo en la tribu Paniceae otros géneros, como por ejemplo *Alloteropsis* y *Panicum*, que incluyen especies C_3 y C_4. Idéntica variación fue reportada por Ellis (1984) para el género *Eragrostis* Wolf, el cual incluye hasta el momento una única especie no-Kranz, *E. walteri*. Ellis (1984) señaló que todos los representantes de la subfamilia Eragrostoideae son Kranz, y que *E. walteri* podría representar un ejemplo de reversión en la evolución del síndrome de Kranz en la subfamilia. Este autor mencionó que un fenómeno similar puede haber ocurrido dentro de las Panicoideas C_4, señalando: "However, this also implies that caution is called for in emphasizing anatomical characteristics of the Kranz syndrome when making taxonomic decisions."

Consecuentemente, se considera prematuro el establecimiento de un nuevo género sobre la base de caracteres anatómicos, existiendo uniformidad en los caracteres exomorfológicos, al menos hasta la obtención de nuevos datos cariológicos o embriológicos.

Posicion Sistematica de *S. Acuminata* y *S. Robusta*

Finalmente, y de acuerdo con la delimitación previa del género *Streptostachys*, se deben excluir del mismo a *S. acuminata* y *S. robusta* por las siguientes razones:

Streptostachys acuminata carece de raquilla engrosada, posee lígula membranáceo-ciliada y antecio superior transversalmente rugoso y crestado, con papilas verrugosas en toda su superficie. Anatómicamente es una planta Kranz, del subtipo PS, con numerosos cloroplastos especializados en la vaina parenquimática.

Ellis (1977) y Prendergast & Hattersley (1987) distinguieron dentro de la categoría anatómica PS los subtipos NAD-me y PEP-ck, definiendo al último por poseer cloroplastos especializados centrífugos en las células Kranz, vaina Kranz de contorno irregular (en particular en los haces vasculares secundarios), y pared tangencial externa marcadamente convexa en las células Kranz. Estos caracteres se observan en el material examinado de *S. acuminata*, aunque la posición de los cloroplastos, si bien es aparentemente centrífuga, se debe considerar dudosa por las características del material examinado.

Streptostachys robusta es una planta no-Kranz, con mesófilo sin células fusoides. La espiguilla carece del típico engrosamiento de la raquilla, posee lígula membranácea y laciniada en la porción apical, láminas pseudopecioladas, espiguilla comprimida lateralmente, y gluma inferior $\frac{4}{5}$ del largo de la espiguilla y con largos pelos hacia el ápice. Desafortunadamente el material en que se basó la nueva especie es inmaduro, por lo que no se pueden apreciar con claridad los caracteres del antecio superior. No obstante, fue posible ver en determinadas espiguillas dos pequeños apéndices, o aurículas, membranosos en la base de la lemma superior. Este carácter, sumado al tipo de lámina, compresión de la espiguilla, y largo relativo y pilosidad de la gluma inferior, permiten suponer que la especie puede pertenecer al género *Ichnanthus*. Sin embargo, y dado que no fue posible relacionar a la misma con alguna de las especies tratadas en la monografía de Stieber (1982, 1987), se ha considerado inapropiado efectuar una nueva combinación sobre la base de material incompleto, por lo que esta especie debe ser excluida del género *Streptostachys* y su posición considerada momentáneamente dudosa.

Los caracteres distintivos de las cinco especies incluídas hasta el presente en *Streptostachys* han sido resumidos en la Tabla 1.

Tratamiento Taxonomico

Streptostachys Desv., Nouv. Bull. Sci. Soc. Philom. Paris 2: 187–190. 1810. ESPECIE TIPO: *S. asperifolia* Desv.

Plantas perennes, cespitosas, con cañas decumbentes y ramificadas en los nudos inferiores a erectas. Hojas con lígulas ciliadas o ausentes; láminas ovado-lanceoladas a lanceoladas, planas, de pilosidad variable. Inflorescencias terminales laxas, con espiguillas solitarias o apareadas; panojas axilares presentes o ausentes. Espiguillas desarticulándose por debajo de las glumas, comprimidas dorsiventralmente, elipsoides, densamente hirsutas o glabras, con raquilla engrosada y manifiesta entre la gluma inferior y el antecio superior, incurva o no en la porción basal; gluma inferior $\frac{1}{6}$–$\frac{4}{5}$ del largo de la espiguilla (1)3–5(7)-nervia, gluma superior y lemma inferior subiguales, gluma superior 5–7-

TABLE 1. Caracteres comparativos de las especies tratadas hasta el presente en *Streptostachys*.

	S. asperifolia	*S. acuminata*	*S. macrantha*	*S. ramosa*	*S. robusta*
Raquilla engrosada	+	−	+	+	−
Hilo linear	+	?	+	+	?
Tipo de lígula	ciliada a ausente	membranaceo-ciliada	ciliada a ausente	ciliada a ausente	membranaceo-laciniada
Ornamentación del antecio superior	liso, piloso y papiloso	transversal-mentrugoso, olabro	liso, piloso y papiloso	liso piloso y papiloso	liso, sin papilas, glabro
Aurículas	−	−	−	−	+
Anatomía foliar	no-Kranz	Kranz, PS	Kranz, MS	Kranz, MS	no-Kranz
Células fusoides	+	−	−	−	−
Pseudopeciolo	Ausente	Ausente	Ausente	Ausente	Presente
Compresión de la espiguilla	Comprimida dorsiven-tralmente	Comprimida dorsiventral-mente	Comprimida dorsiventral-mente	Comprimida dorsiventral-mente	Comprimida lateralmente

nervia, lemma inferior (3)5–7-nervia; pálea inferior conspicua, de tamaño similar a la lemma inferior, glabra, a reducida o ausente; flor inferior masculina o ausente; antecio superior elipsoide, endurecido, liso, piloso, con pelos uni- o bicelulares sobre toda la superficie, con papilas simples distribuidas regularmente; lodículas 2, truncadas, conduplicadas, abrazando los bordes inferiores de la pálea; estambres 3; estilos libres, estigmas plumosos; cariopsis con hilo linear ocupando todo el largo de la cariopsis, embrión menos de ½ del largo de la cariopsis.

Género americano con tres especies, incluyendo, además de la especie tipo, a *S. macrantha* y *S. ramosa*.

CLAVE DE LAS ESPECIES

1a. Panoja terminal y axilares numerosas saliendo en abanico en el extremo de las cañas. Espiguillas de 3.6–5.1 mm de largo, raquilla con los bordes inferiores involutos. Gluma inferior ⅔–⅘ del largo de la espiguilla. Planta no-Kranz con células fusoides ..... 1. *S. asperifolia*

1b. Panojas axilares ausentes. Espiguillas de 5.9–9.3 mm de largo, raquilla con los bordes inferiores rectos. Gluma inferior ⅙–⅔ del largo de la espiguilla. Plantas Kranz, MS, células fusoides ausentes.

2a. Plantas de 30–70 cm de alto. Láminas de 7–14 cm de largo, 0.7–1.3 cm de ancho. Panojas de 5–10 cm de largo. Transcorte de la hoja con zonas costales e intercostales poco marcadas; estomas abaxiales no hundidos y no cubiertos por papilas. ..... 2. *S. macrantha*

2b. Plantas de 1.3–2 m de alto. Láminas de 35–60 cm de largo, 1–1.4 cm de ancho. Panojas de 30–45 cm de largo. Transcorte de la hoja con zonas costales e intercostales marcadas; estomas abaxiales hundidos y cubiertos por papilas ..... 3. *S. ramosa*

1. Streptostachys asperifolia Desv., Nouv. Bull. Sci. Soc. Philom. Paris 2: 190. 1810. *Panicum asperifolium* (Desv.) A. Hitchc., Contr. U.S. Natl. Herb. 22: 489. 1922. *Panicum streptostachys* Sprengel, Syst. Veg. 1: 316. 1825. *Streptostachys hirsuta* P.Beauv., Ess. Agrost.: 50, pl. 10, f. 11, 1812. TIPO: "Habitat in America (guian.)," *Desvaux s.n.* (holotipo, P; fragmento, US).

Panicum perfoliatum Nees, Agrost. Bras.: 142. 1829. TIPO: Brasil. Piauí: "Habitat in graminosis in de Serra dos dois Irmãos ad Oeiras usque ad Provinciae Piauhiensis," *Martius s.n.* (holotipo, M; isotipo, M).

Panicum balanites Trin., Linnaea: 297. 1836. TIPO: Brasil. Amazonas: Colares, *Poeppig s.n.* (holotipo, LE n.v.; isotipos, US, W).

Panicum vaginaeflorum Steudel, Syn. Pl. Glumac. 1: 80. 1854. TIPO: Guyana Francesa: sin localidad y colector (holotipo, P; fragmento, K).

Plantas perennes, cortamente rizomatosas, cañas decumbentes, arraigadas en los nudos inferiores, luego erectas, de 25–100 cm de alto, ramificadas en los nudos superiores; entrenudos huecos, cilíndricos; nudos comprimidos, pubescentes o glabros. Vainas de 4.5–10 cm de largo, densamente hirsutas o glabras, los márgenes pestañosos; lígulas ciliadas, de 1–1.8 mm de largo, o ausentes; láminas ovado-lanceoladas, de 10–28 cm de largo, 1.8–4.3 cm de ancho, planas, cordadas y amplexicaules, densamente hirsutas o glabras, los bordes basales ciliados con largos pelos blanquecinos, tuberculados. Inflorescencias terminales de 6–16 cm de largo, 1–9 cm de ancho, oblongas a piramidales, largamente pedunculadas; eje principal esparcidamente piloso a glabro, racimos divergentes, alternos, ejes de las ramificaciones esparcidamente pilosos a escabrosos, triquetros, espiguillas en pares

sobre ambos lados del eje; pedicelos cortos, angulosos, escabrosos, ocasionalmente con largos pelos blanquecinos. Panojas axilares numerosas, similares a la panoja terminal. Espiguillas elipsoides, de 3.6–5.1 mm de largo, 1.2–1.9 mm de ancho, densamente hirsutas o glabras, con raquilla conspicua y engrosada entre la gluma inferior y el antecio superior, los bordes inferiores involutos y rodeando el ápice del pedicelo. Gluma inferior oblonga, obtusa, de 3–4.7 mm de largo, ⅔–⅘ del largo de la espiguilla, 5–7-nervia, con nervios anastomosados hacia el ápice. Gluma superior de 2.7–4.7 mm de largo, dejando libre el ápice del antecio superior, 5–7-nervia, obtusa. Lemma inferior 5-nervia, membranácea a endurecida y cubriendo con los bordes al antecio superior. Pálea inferior de 1.3–2.4 mm de largo, 0.4–0.7 mm de ancho, castaña a blanquecina, hialina, glabra, o ausente; flor inferior ausente. Antecio superior elipsoide, de 3–3.9 mm de largo, 1.3–1.6 mm de ancho, pajizo, liso, con papilas simples distribuidas regularmente, piloso hacia la porción superior; lodículas abrazando los bordes inferiores de la pálea; estambres 3, anteras de 2.4 mm de largo; estilos libres, estigmas plumosos. Cariopsis de contorno oblongo, de 2.4–2.8 mm de largo, 1.2–1.3 mm de ancho, pajizo a castaño; hilo linear, ocupando todo el largo de la cariopsis, embrión menos de ½ del largo de la cariopsis.

Distribución. Se encuentra desde Trinidad y Venezuela por las Guyanas hasta el norte de Brasil.

Material representativo examinado. BRASIL. AMAPÁ: estrada de rodagem Macapá e Clevelandia, entre os kms 106 e 110, *Black & Froes 51-12407* (IAN); 2 km from Rio Araguarí, along road from Porto Platon to Macapá, *Pires et al. 51084* (K, US); Porto Platón, *Mattos 10120* (SP, US); Calcoene, road to gold mines, *Pires & Cavalcante 52520* (K, NY); estrada Fazendinha entre os kms 8 e 14, *Black & Froes 51-12330* (IAN); Macapá, *Black & Froes 51-12279* (IAN); Matapí, *Pires & Silva 4799* (IAN, P). AMAZONAS: sin localidad, *Martius s.n.* (M). BAHIA: Bom Jesús, *Luetzelburg 416* (M, NY), *1913** (NY); Grameal Nanica, *Black 54-17938* (IAN); Serra do Aporá, *Pinto 256* (IAN); 16 km NW of Lagoinha, on side road to Minas do Mimoso, *Harley et al. 16642* (P). CEARA: Granjeiro, Taboleiros, *Luetzelburg 26008, 26507* (M); Quixadá, Fazenda Normal, *Black 55-18473* (IAN). GOIAS: 2 km N of Araguainia, *Irwin et al. 21133* (F, K, NY, US). MARANHÃO: 20 km ao sudeste de São João dos Patos ao longo da BR-230, *Valls et al. 8450* (CEN); São Luiz, Granja Barreto, *Froes 24312* (IAN, P, SP); Carema, *Froes 25860* (IAN); Itapicurú, *Black et al. 54-16679* (IAN); Alcántara, Periuasinho, *Froes 30794* (IAN). PARÁ: near Soure, Marajó Island, *Goeldi 299* (F, SP, US, W); Marabá, Serra dos Carajás, *da Silva 1868* (SP); Marabá, arredores do N5, *Secco et al. 467* (K); Caracara River, Marajó Island, *Goeldi 99* (W); Belem, Rio Guajará, *Black 54-16163* (IAN); Ilha de Colares, *Black 54-17015* (IAN); capoeira de Condeixa, Ilha de Marajó, *Black 48-3584* (IAN); camino de Jubim para Condeixa, Ilha de Marajó, *Black 48-3549* (IAN); estrada de Salvaterra para Jubim, Ilha de Marajó, *Black 48-3507* (IAN); estrada de rodagem para Vigia, *Froes 27819* (IAN); Santarem, *Maciel & Cordeiro 335** (NY), *Spruce 606, 697* (P), *Swallen 3267* (K, P, W) *Pires & Black 1137* (IAN), *Black & Ledoux 50-10273* (IAN); Marajó, *Rosa et al. 924* (NY). PERNAMBUCO: Paulista, *Tenoiro 66/151* (M). PIAUÍ: sin localidad, *Gardner 2341* (P, W); 32.8 km along road south of Aramante, *Eiten & Eiten 10371* (P); Calverao, *Luetzelburg 410* (P). RIO GRANDE DO NORTE: João Pessoa, *Sarmento & Assis 750** (NY). GUYANA. Sin localidad, *Schomburgk 774* (W). GUYANA FRANCESA: Region de Cayenne, route entre le Gallion et Montsinery, *Descoings & Luu 20217* (P); route du tour de L'Ile, *Veyvret & Cremers 4392* (P); Ile de Cayenne, route de la Chaumiere, *de Granville BC.75* (P); Cayenne, route de Rochambeau, *Hoock 103* (P); estrada Sinnamary-Iracoubo, km 13, *Black & Klein 54-17392** (IAN); campo a 10 km de Cayenne, *Black & D'Aage 54-18173* (IAN); Route de Sinnamary, *Hoock s.n.* (IAN 95073); Cayenne, *Sagot 1395* (P, W). SURINAM: Zuid Rivier, 25 km above confluence with Lucie Rivier, *Maguire et al. 53953** (P, SI); Kayserberg airstrip on the Zuid Rivier, *Kramer & Hekking 2979** (NY); Kayser airstrip, *Irwin et al. 55991** (F, P). VENEZUELA. ANZOATEGUI: bosques cercanos a Playa Colorada, a unos 25 km de Puerto La Cruz, vía Cumaná, *Aristeguieta & Labbiente 7303* (MO). BOLÍVAR: Isla en el lago de Guri (sector Las Carolinas), 15 km al E de la presa R. Leoni, *Aymard et al. 7648* (MO). SUCRE: 7 km E of the Mochima Hwy. intersection along Hwy. 9 between Cumaná and Puerto La Cruz, *Davidse 5044* (MO).

CARACTERES HISTOFOLIARES EN CORTE TRANSVERSAL (FIGS. 2A, B; 3A)

Transcorte plano, de 200–290 μm de espesor, zonas costales e intercostales suavemente pronunciadas; costilla central con un haz vascular primario asociado a células parenquimáticas incoloras hacia la cara adaxial y solitario o asociado a haces vasculares secundarios; 4–6 haces vasculares secundarios entre haces vasculares primarios contíguos, hallándose ambos tipos de haces en correspondencia con las zonas costales; haces vasculares adyacentes a una distancia de 330–350 μm y separados por aproximadamente 12 células clorenquimáticas. Haces vasculares primarios de contorno circular, trabados, rodeados por 2 vainas, la interna mestomática y la externa parenquimática, ambas sin cloroplastos especializados; vaina parenquimática contínua, compuesta por 15–21 células globosas. Haces vasculares secundarios de contorno angular, trabados; vaina parenquimática contínua, de 8–10 células; vaina mestomática completa. Clorénquima irregularmente radiado alrededor de los haces vasculares, con células tabulares, raquimorfas, dispuestas en dos capas hacia la cara adaxial, y con células isodiamétricas hacia la cara abaxial; por debajo de las células buliformes

con células clorenquimáticas tabulares distribuidas regularmente y semejando un tejido en empalizada, con abundantes cloroplastos en relación al resto del tejido clorenquimático; "arm cells" presentes, próximas a la cara abaxial; espacios intercelulares presentes. Células fusoides presentes. Células buliformes en grupos regulares de 4–5 células "tipo abanico" presentes en las zonas intercostales adaxiales. Esclerénquima hipodérmico, en correspondencia con los haces vasculares primarios y secundarios y el margen foliar. Cristales ausentes. Amiloplastos presentes en las células clorenquimáticas.

CARACTERES EPIDÉRMICOS DE LA LÁMINA EN VISTA PARADERMAL (FIG. 2C)

Zonas costales con cuerpos de sílice halteriformes, alternando con células suberosas rectangulares; aguijones ausentes. Zonas intercostales con células largas rectangulares, longitudinalmente alargadas, más de tres veces más largas que anchas, de paredes onduladas; células cortas en pares sílico-suberosos. Aparatos estomáticos romboidales a subdiscoidales, de 30–46 μm de largo, 22.5–25.5 μm de ancho, distribuidos en las zonas intercostales en 2–6 hileras, menos frecuentes en la cara adaxial. Ganchos no vistos. Micropelos 2-celulares, fusiformes, de 45–52.5 μm de largo, célula basal más corta que la distal, célula distal de paredes delgadas y ápice obtuso. Macropelos unicelulares, de 600–900 μm de largo, de paredes engrosadas, base bulbosa y ápice largamente atenuado, asociados a células epidérmicas sobreelevadas con respecto al resto de la epidermis. Papilas ausentes.

Observaciones. Diversos autores, como Metcalfe (1960), Jacques-Félix (1962), y Soderstrom & Ellis (1987) señalaron la presencia en el mesófilo de células fusoides como un carácter distintivo de la subfamilia Bambusoideae.

Las células fusoides de las Bambusoideae son, en corte transversal, fusiformes, de lumen amplio y traslúcidas, de posición lateral con respecto al haz vascular, y se hallan en contacto directo con las células de la vaina externa de los haces vasculares. En corte longitudinal se presentan estrechas, con escaso lumen celular, ligeramente más amplio hacia ambas caras epidérmicas, y están separadas unas de otras por conspicuos espacios intercelulares (Metcalfe, 1960; Calderón & Soderstrom, 1973; Ellis, 1976). Soderstrom et al. (1987) diferenciaron a las células fusoides de la tribu Phareae por presentarse, cuando maduras, globosas, transversalmente alargadas, y con paredes excepcionalmente delgadas, no dejando conspicuos espacios entre si en corte longitudinal.

Watson et al. (1985) y Watson & Dallwitz (1988) mencionaron la presencia de células fusoides en el género *Homolepis* dentro de la supertribu Panicanae. Indicaron como posible una evolución paralela o convergencia del carácter en las subfamilias Bambusoideae y Panicoideae.

Killeen & Clark (1986) reconocieron "fusoid-like cells" en especies de la sección *Laxa* del género *Panicum*. De acuerdo con estos autores, estas células eventualmente no deberían ser consideradas homólogas a las células fusoides presentes en la subfamilia Bambusoideae.

Renvoize (1987) señaló células fusoides en dos géneros de Paníceas, *Homolepis* y *Streptostachys*.

Al estudiar estas células en *S. asperifolia* se observó que las mismas difieren de las células fusoides previamente descriptas para la generalidad de las Bambusoideae, por ser en corte longitudinal más o menos cuadradas, con lumen celular amplio y por presentar escasos espacios intercelulares entre células fusoides contíguas. De acuerdo con esta descripción, dichas células coinciden con las mencionadas por Soderstrom et al. (1987) para la tribu Phareae.

En el presente trabajo se mantiene el término de fusoides para las células presentes en *S. asperifolia*, hasta tanto se efectúen estudios ontogenéticos comparados entre taxa de las subfamilias Bambusoideae y Panicoideae.

2. Streptostachys macrantha (Trin.) Zuloaga & Soderstrom, Smithsonian Contr. Bot. 59: 50. 1985. *Panicum macranthum* Trin., Gram. Panic.: 209. 1826. TIPO: Brasil, sin localidad, *Langsdorff s.n.* (holotipo, LE n.v.; isotipo, K; fragmento del tipo, US). Figure 1A–K.

Panicum vaginatum var. *alpha* et *beta* Nees, Agrost. Bras.: 156. 1829. TIPO: Brasil, sin localidad, *Sellow s.n.* (holotipo, B n.v.; isotipo, K; fragmento, US).

Plantas perennes, cortamente rizomatosas, con rizomas fuertes cubiertos de catáfilos vilosos; cañas de 30–70 cm de alto, simples, con hojas basales numerosas y manifiestamente dísticas, cañas floríferas de 2–3 nudos y con hojas con láminas reducidas; entrenudos comprimidos, glabros; nudos oscuros, pilosos o glabros. Vainas rala o densamente pilosas, cuello pajizo a violáceo, piloso o glabro. Lígulas ciliadas o ausentes. Láminas lanceoladas, acuminadas, de 7–14 cm de largo, 0.7–1.3 cm de ancho, verde oscuras, rígidas, atenuadas o cordadas. Inflorescencias terminales laxas, de 5–10 cm de largo, 2–7 cm de ancho; eje principal an-

guloso, glabro, ramificaciones inferiores verticiladas o alternas, las superiores alternas, divergentes, con espiguillas solitarias sobre pedicelos cortos; pedicelos glabros, convexos. Espiguillas elipsoides, de 5.9–7.4 mm de largo, 2.1–2.5 mm de ancho, verdosas y con tintes violáceos, pilosas sobre el ápice de la gluma superior y lemma inferior o glabras, con raquilla conspicua y engrosada entre la gluma inferior y el antecio superior. Gluma inferior ovada, de 2.3–4.7 mm de largo, ⅓–⅔ del largo de la espiguilla, 1–3-nervia, nervio medio escabroso hacia el ápice. Gluma superior de 5–6.6 mm de largo, dejando libre el ápice del antecio superior, 5–7-nervia, los nervios anastomosados hacia el ápice. Lemma inferior de 5.4–6.7 mm de largo, 3–5-nervia. Pálea inferior lanceolada, de 4.3–5.8 mm de largo, 1–1.6 mm de ancho, hialina, glabra; flor inferior presente, lodículas 2, truncadas, conduplicadas, estambres 3, anteras de 4.2 mm de largo. Antecio superior ovoide, de 5.1–5.9 mm de largo, 1.8–2.4 mm de ancho, pajizo, liso y lustroso, piloso y papiloso; lodículas de 0.7 mm de largo, abrazando los bordes inferiores de la pálea; estambres 3, anteras violáceas de 3.8 mm de largo; estigmas emergiendo por el ápice del antecio superior. Cariopsis fusiforme, de 3.6 mm de largo, 1.7 mm de ancho, hilo linear, ocupando todo el largo de la cariopsis, embrión menos de ½ del largo de la cariopsis.

Distribución. Brasil, en el Distrito Federal y los estados de Goiás y Minas Gerais, hallándose ocasionalmente en Paraguay en la Sierra de Amambay. Habita en cerrados sujetos a fuegos periódicos, en suelos pedregosos. Llega hasta aproximadamente 1,200 m. Florece entre octubre y diciembre.

Material representativo examinado. BRASIL. DISTRITO FEDERAL: in the area of the Córrego Cabeça do Veado, ca. 9.5 km SSE of Brasilia TV tower, *Ratter et al. 3355* (K, UB); 20 km S of Brasilia on road to Goiania, near Rio Melchior, *Irwin et al. 8658** (US); proximidades da Escola Fazendaria, *Heringer 18255* (IBGE); Fazenda Santa Prisca, *Heringer et al. 2018* (IBGE); Lago Norte, *Filgueiras 769, 778, 790* (IBGE); Lago Sul, proximidades do Córrego Taquarí, *Heringer et al. 7510* (IBGE). GOIÁS: Pichoa, *Glaziou 22526* (G, K, M, P, W); 33 km S of Caiaponia on road to Jataí, *Irwin & Soderstrom 7131* (F, K, MO, UB, US*); Cristalina, *Filgueiras & Pereira 923* (IBGE); Serra do Caiapó, 30 km N of Jataí on road to Caiaponia, *Irwin & Soderstrom 7307* (K, US); Luziania, *Heringer 13963* (IBGE, UB); Chapada dos Veadeiros, *Heringer et al. 2754* (IBGE); sin localidad, *St. Hilaire 660* (P). MINAS GERAIS: 37 km S of Prata on highway BR-14, *Goodland 3967* (UB); Serra do Cipó, 110 km NE of Belo Horizonte, *Chase 9297** (US); Morro do Cruzeiro, Lagoa Santa, 42 km N of Belo Horizonte, *Chase 9018** (NY, US); Paracatú, *Filgueiras & Pereira 924, 925* (IBGE); estrada de Cristalina a Paracatú, *Heringer & Rizzini 17447* (IBGE); Rio São Francisco, *Pohl 329** (M, W, US); ad Lagoa Santa, *Warming s.n.* (M, W); sin localidad, *St. Hilaire 473* (P), *Riedel s.n.* (P, W), in campis inter Catalão et Paracatú, *Lund 1834* (W). PARAGUAY: Sierra de Amambay, in campis arenosis Estrella, *Hassler 10115* (BAA, G).

Observaciones. En K hay un ejemplar de Brasil: Minas Gerais, in campis Lagoa Santa, *Riedel 2152*, que pertenece a la especie y que ha sido identificado en ese herbario como un isotipo de la misma. Cabe destacar que Renvoize (1978) indicó que determinados ejemplares coleccionados por Riedel en su viaje con Langsdorff por el Brasil deben ser considerados como de la misma colección hecha por el último autor (y sobre la que Trinius basó la mayor parte de sus descripciones en Paníceas).

CARACTERES HISTOFOLIARES EN CORTE TRANSVERSAL (FIG. 2D, E)

Transcorte plano, de 200–350 μm de espesor; zonas costales e intercostales suavemente pronunciadas; costilla central no diferenciada; 3–4 haces vasculares secundarios, 4–6 haces vasculares terciarios y 2–3 haces vasculares cuaternarios entre haces vasculares primarios contíguos, haces vasculares adyacentes a una distancia de 60–150 μm y separados por 2–3 células clorenquimáticas. Haces vasculares primarios de contorno elíptico, trabados, y equidistantes de ambas epidermis, en correspondencia con las zonas costales, rodeados por una vaina mestomática Kranz compuesta por 13 a 20 células; células Kranz globosas en corte transversal, de tamaño igual o menores que las células clorenquimáticas adyacentes, y rectangulares en vista paradermal, con su eje mayor paralelo a las venas, con cloroplastos especializados de posición centrífuga u ocupando todo el lumen celular, células de la vaina de paredes radiales y tangencial externa curvas, con paredes igualmente engrosadas o con las paredes radiales y tangencial interna manifiestamente engrosadas; 1 hilera de células esclerenquimáticas presente o ausente entre la vaina mestomática y los elementos del metaxilema. Haces vasculares secundarios de contorno elíptico, trabados y equidistantes de ambas epidermis, con 9–15 células en la vaina Kranz. Haces vasculares terciarios libres, dispuestos hacia la cara abaxial, de contorno angular, asociados a las zonas intercostales, con 6–8 células en la vaina Kranz. Haces vasculares cuaternarios libres, próximos a la cara abaxial, de contorno cuadrado, asociados a las zonas intercostales, con 4 células en la vaina Kranz. Clorénquima irregularmente radiado con células

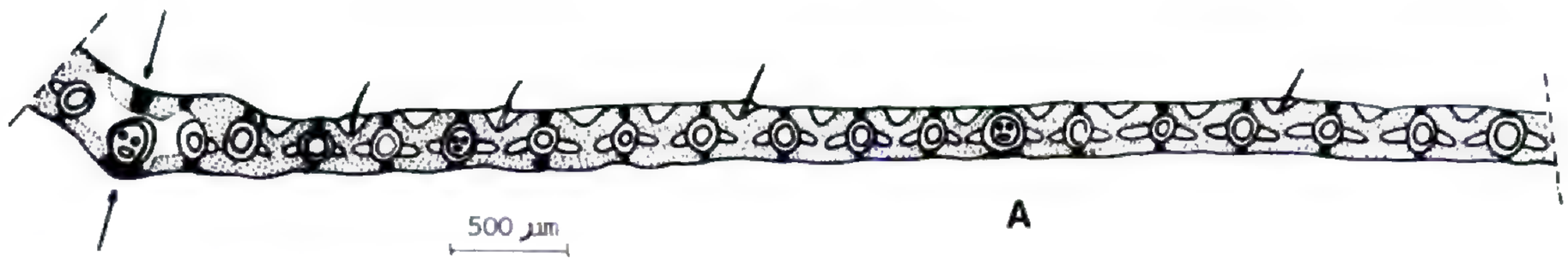

FIGURA 2. A–C. *Streptostachys asperifolia*.—A. Transcorte de una porción de la semilámina mostrando la costilla central (flechas).—B. Detalle de la semilámina en transcorte, entre un haz vascular primario y secundario.—C. Detalle de la epidermis abaxial. D–F. *Streptostachys macrantha*:—D. Aspecto general de un fragmento de la semilámina en transcorte, señalando nervio medio (flechas).—E. Detalle de la semilámina en transcorte.—F. Detalle de la epidermis abaxial. G–I. *Streptostachys ramosa*.—G. Aspecto general de un fragmento de semilámina en transcorte.—H. Detalle de la semilámina en transcorte.—I. Detalle de la epidermis abaxial. a, haz vascular primario; b, haz vascular secundario; c, haz vascular terciario; d, haz vascular cuaternario; f, célula fusoide. (A–C de *Irwin et al. 55991*; D–F de *Irwin et al. 8658*; G–I de *Harley et al. 16876*.)

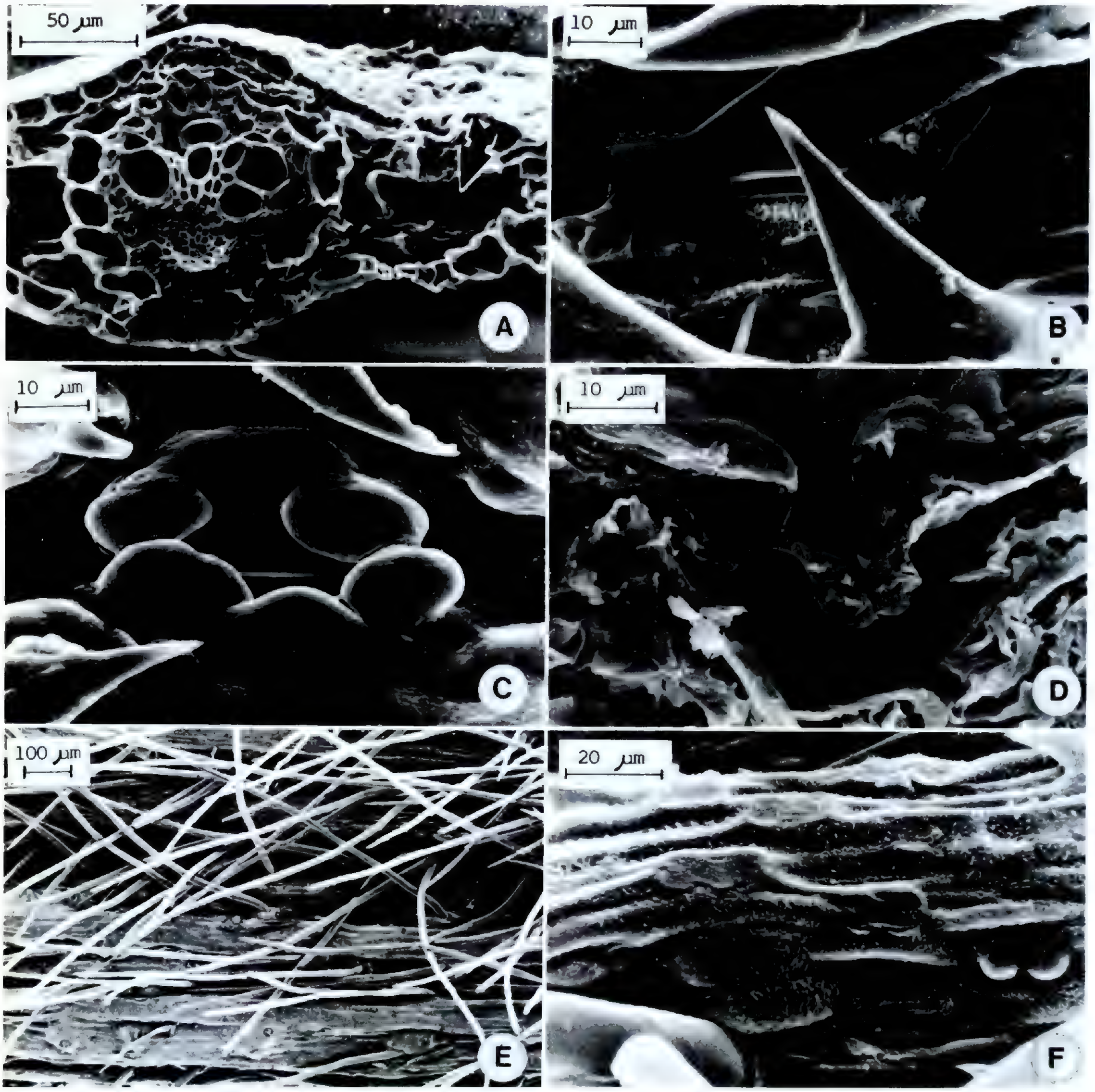

FIGURA 3. *Streptostachys asperifolia.*—A. Detalle de una porción de la semilámina en transcorte, con un haz vascular primario y células fusoides (flecha). B–D. *Streptostachys ramosa.*—B. Detalle de la zona intercostal adaxial.—C. Detalle de la epidermis abaxial, con aparato estomático, cubierto por papilas.—D. Transcorte de C. E, F. *Streptostachys macrantha*:—E. Epidermis abaxial.—F. Detalle de la zona costal abaxial. (A de *Kramer & Hekking 2979*; B–D de *Filgueiras 855*; E, F de *Irwin et al. 8658.*)

rectangulares alrededor de los haces vasculares, y con células isodiamétricas en el resto del mesófilo; espacios intercelulares escasos. Células fusoides ausentes. Células buliformes en grupos de 4–6 células, tipo "abanico" presentes en las zonas intercostales. Parénquima incoloro distribuido por debajo de las células buliformes. Esclerénquima poco desarrollado, hipodérmico, en correspondencia con los haces vasculares primarios y secundarios y el margen foliar. Cristales ausentes. Amiloplastos presentes en las vainas mestomáticas Kranz.

CARACTERES EPIDÉRMICOS DE LA LÁMINA EN VISTA PARADERMAL (FIGS. 2F; 3E, F)

Zonas costales con cuerpos de sílice halteriformes, menos frecuentemente nodulares; aguijones presentes en la cara adaxial. Zonas intercostales con células largas rectangulares, alargadas longitudinalmente, hasta tres veces más largas que anchas, de paredes ligeramente onduladas; células cortas solitarias o en pares. Aparatos estomáticos romboidales, de 33–36 µm de largo, 22–27 µm

de ancho, dispuestos en 2 hileras en las zonas intercostales. Ganchos presentes. Micropelos 2-celulares, fusiformes, de 52.5–72 μm de largo, célula distal más larga que la basal, de paredes delgadas y ápice redondeado. Macropelos unicelulares, presentes en la cara adaxial, de 300–600 μm de largo, rígidos, de paredes engrosadas, base bulbosa y ápice agudo, asociados a células epidérmicas no sobreelevadas. Papilas ausentes.

Observaciones. A pesar de hallarse esta especie en un habitat similar al de *S. ramosa*, *S. macrantha* carece de las adaptaciones xeromórficas presentes en esa especie.

3. Streptostachys ramosa Zuloaga & Soderstrom, Smithsonian Contr. Bot. 59: 52. 1985. TIPO: Brasil. Bahia: 22 km S of the Rio Galheirao along highway BR-020, 8 Apr. 1976, 860 m, *Davidse et al. 12216* (holotipo, MO; isotipos, NY, SP).

Planta perenne, fuertemente rizomatosa; cañas de 1.30–2 m de alto, simples, con hojas basales numerosas, cañas floríferas de 2–3 nudos, entrenudos cilíndricos, glabros, huecos, sólidos en la porción inferior de las cañas; nudos oscuros, comprimidos, glabros. Vainas estriadas, densamente vilosas o glabras, los bordes cortamente pilosos, cuello glabro o cortamente piloso. Lígulas ciliadas, de 0.8–2.5 mm de largo, o ausentes. Láminas lanceoladas, de 30–60 cm de largo, 1–1.4 cm de ancho, planas o con los bordes involutos, lisos, subcordadas, densamente hirsutas en ambas caras o escabriúsculas en la cara adaxial y glabras en la cara abaxial. Pedúnculos de aproximadamente 70 cm de largo. Inflorescencias terminales laxas, piramidales de 30–45 cm de largo, 15–30 cm de ancho; eje principal cilíndrico, glabro, ramificaciones inferiores verticiladas, ocasionalmente alternas, las superiores verticiladas a subopuestas, divergentes del eje principal, eje de las ramificaciones glabro, axilas de las ramificaciones densamente pilosas; espiguillas solitarias y dispuestas unilateralmente sobre las ramas, ramificaciones de tercer orden presentes o más comúnmente ausentes; pedicelos glabros, convexos. Espiguillas largamente elipsoides, de 6.3–9.3 mm de largo, 2.1–2.7 mm de ancho, glabras, verdosas y con tintes violáceos, raquilla manifiesta y engrosada entre la gluma inferior y el antecio superior. Gluma inferior de 1.5–4.4 mm long., ⅙–½ del largo de la espiguilla, aguda, 1–3-nervia, cortamente pilosa en el ápice. Gluma superior obtusa a aguda, 5–7-nervia. Lemma inferior 3–5(7)-nervia, cortamente pilosa en el ápice de la cara interna. Pálea inferior lanceolada, de 5.3–7.9 mm de largo, 1–2.2 mm de ancho, membranácea, glabra; flor inferior presente, lodículas 2, truncadas, estambres 3, anteras de 4.3 mm long. Antecio superior elipsoide, de 5.4–7.9 mm de largo, 1.9–2.4 mm de ancho, blanquecino, piloso y papiloso; lodículas abrazando los bordes inferiores de la pálea. Cariopsis fusiforme, de 3.8 mm de largo, 1.7 mm de ancho, hilo linear, ocupando todo el largo de la cariopsis, embrión menos de ½ del largo de la cariopsis.

Distribución. Brasil, en cerrados de los estados de Bahia, Goiás, Minas Gerais, y Mato Grosso, a 400–1,500 m. Crece en suelos arenosos, pedregosos. Florece entre enero y abril.

Material representativo examinado. BRASIL. BAHIA: Ipatá, *Harley et al. 24147* (K); Mucugé, rodovía para Palmeira, *Hatschbach & Kummrow 48033* (K); Serra do Sincorá, ca. 15 km NW of Mucugé on the road to Gune & Palmeiras, *Harley et al. 20997* (K); 15 km S of the intersection of highway BR-020 and the Rio Roda Velha, *Davidse et al. 12085* (K, MO, NY, SP, US*); Serra do Curral Feio, 22 km NW of Lagoinha, on side road to Minas do Mimoso, *Harley et al. 16876* (K, MO, NY, P, US*); Espigão Mestre, ca. 100 km WSW of Barreiras, *Anderson et al. 36657* (MO*, NY, UB). GOIÁS: Rodovía BR-050, Mun. Campo Alegre de Goiás, *Hatschbach 51776* (K); Cristalina, 29-I-1980, *Heringer & Rizzini 17626* (IBGE). MATO GROSSO: Chapada dos Guimaraes, *Hatschbach et al. 36145* (K, MO, NY), *Filgueiras 855* (IBGE); entre Aldeia Quemada e Rio Verde, Mar. 1921, *Kuhlmann s.n.* (RB, SI*). MINAS GERAIS: Mun. Francisco Sá, Serra do São Calixto, *Burman 147*, *185*, *195* (SP): ca. 20 km S of Alto do Paraiso, *Irwin et al. 24716* (NY*).

Número cromosómico. $n = 27$ (Davidse & Pohl, 1978, bajo *Panicum macranthum* Trin.).

Observaciones. *Streptostachys ramosa* se aparta exomorfológicamente de *S. macrantha* por el mayor tamaño de plantas, láminas y panojas.

En el ejemplar *Glaziou 20123a* (K, P), figura como lugar de colección Río de Janeiro, Brasil, lo cual obviamente es un error de etiquetado dada la distribución y el hábitat donde crece la especie.

CARACTERES HISTOFOLIARES EN CORTE TRANSVERSAL (FIGS. 2G, H; 3D)

Transcorte en forma de "U" abierta, involuto, de 360–440 μm de espesor; cara adaxial con zonas costales conspícuas, de ápice truncado y zonas intercostales hasta ½ de profundidad en relación al ancho de la lámina; cara abaxial con zonas costales e intercostales poco manifiestas; costilla central conspicua; 2–4 haces vasculares secundarios, 4–8 haces vasculares terciarios y 2–6 haces vasculares cuaternarios entre haces vasculares pri-

marios contíguos; haces vasculares adyacentes a una distancia de 60–160 μm y separados por 2–3 células clorenquimáticas. Haces vasculares primarios de contorno elíptico, asociados a las zonas costales, trabados y equidistantes de ambas epidermis, rodeados por una vaina mestomática Kranz, compuesta de 13–25 células de tamaño igual o menor que las células del mesófilo; células Kranz globosas en corte transversal y rectangulares en vista paradermal, con su eje mayor longitudinal; células Kranz con las paredes radiales y tangencial externa curvas, igualmente engrosadas o con las paredes radiales y tangencial interna fuertemente engrosadas; cloroplastos de posición centrífuga u ocupando todo el lumen celular; 1–3 hileras de células esclerenquimáticas de lumen pequeño y paredes igualmente engrosadas presentes o ausentes entre la vaina Kranz y los elementos del metaxilema. Haces vasculares secundarios de contorno elíptico, en correspondencia con las zonas costales, trabados a semitrabados y equidistantes de ambas epidermis, con 10–15 células Kranz globosas a reniformes, con las paredes más o menos igualmente engrosadas, extensiones de la vaina presentes o ausentes, cuando presentes compuestas por 1 o 2 células dispuestas hacia ambas caras. Haces vasculares terciarios libres en correspondencia con las zonas intercostales, dispuestos hacia la cara abaxial, de contorno angular, vaina mestomática con 5–8 células Kranz. Haces vasculares cuaternarios libres, de contorno cuadrado, próximos a la cara abaxial y en correspondencia con las zonas intercostales. Clorénquima irregularmente radiado alrededor de los haces vasculares con células más o menos rectangulares, el resto del clorénquima con células isodiamétricas y con escasos espacios intercelulares. Células fusoides ausentes. Células buliformes en grupos de 2–4 células tipo "abanico" distribuidas en las zonas intercostales adaxiales. Esclerénquima discontínuo, hipodérmico, abundante en las zonas costales en correspondencia con los haces vasculares primarios, secundarios y el margen foliar. Cristales ausentes. Amiloplastos presentes en las vainas mestomáticas Kranz.

CARACTERES EPIDÉRMICOS DE LA LÁMINA EN VISTA PARADERMAL (FIGS. 2I; 3B, C)

Zonas costales con cuerpos de sílice halteriformes; aguijones frecuentes en la cara adaxial. Zonas intercostales con células largas rectangulares, alargadas longitudinalmente, más de tres veces más largas que anchas, de paredes onduladas, fuertemente engrosadas; células cortas solitarias o en pares, rectangulares. Aparatos estomáticos subdistales, de 37–45 μm de largo, 33–39 μm de ancho, distribuidos en 1–4 hileras en las zonas intercostales, en el mismo nivel que el resto de las células epidérmicas en la cara adaxial y hundidos en la cara abaxial. Ganchos y aguijones presentes en las zonas intercostales de la cara adaxial. Micropelos 2-celulares, fusiformes, de 79.5–94.5 μm de largo, con ambas células de aproximadamente igual tamaño; célula basal de paredes engrosadas, célula distal de paredes delgadas y ápice obtuso. Macropelos unicelulares de 750–1,200 μm de largo, de paredes engrosadas, base bulbosa y ápice agudo, asociados a células epidérmicas en el mismo nivel que el resto de la epidermis. Papilas presentes en las zonas intercostales abaxiales, asociadas a las células largas e interestomáticas, de posición distal y excéntrica, cubriendo parcialmente a los estomas.

Observaciones. *Streptostachys ramosa* posee caracteres predominantemente xeromórficos, como ser la presencia de cutícula gruesa, zonas costales e intercostales adaxiales conspicuas (con zonas intercostales profundas), con numerosos aguijones cubriendo los aparatos estomáticos adaxiales, y hallándose a su vez los estomas abaxiales hundidos y cubiertos parcialmente por papilas, siendo este último carácter poco frecuente en la epidermis de las gramíneas.

Eiten (1978) señaló para la región del cerrado (incluyendo a los campos rupestres), una estación seca entre abril y septiembre con aproximadamente 250 mm de precipitación, existiendo en el resto del año una precipitación promedio de 1,350 mm. Los suelos son comúnmente arenosos, bien drenados, y generalmente pobres en nutrientes, siendo la radiación solar intensa en este tipo de ambiente.

ESPECIE EXCLUIDA

El análisis del material típico de *S. acuminata* permitió comprobar que la especie fue casi simultáneamente descripta por Zuloaga & Soderstrom (1985) bajo el nombre de *Brachiaria tatianae*.

Los caracteres diagnósticos del género *Brachiaria* (Trin.) Griseb. han sido cuestionados en los ultimos años por autores como Hsu (1965) y más recientemente por Webster (1987). Este último autor consideró a *Brachiaria* como género monotípico, incluyendo en el mismo únicamente a *B. eruciformis* (J. E. Smith) Griseb. por tener antecio superior liso, punto primario de desarticulación por encima de la gluma inferior, lemma mútica y pálea no cubierta por la lemma en su porción apical. Webster (1987) distinguió a *Urochloa* P. Beauv. por poseer antecio superior rugoso, espiguillas desarticulando por debajo de la gluma in-

ferior, lemma mútica, crestada o apiculada y pálea cubierta por la lemma en su ápice.

Siguiendo el criterio sustentado por Webster (1987, 1988), y por coincidir *S. acuminata* con los caracteres diagnósticos del genero *Urochloa*, en la presente contribución se trata a la especie en el género *Urochloa*.

Urochloa acuminata (Renvoize) Morrone & Zuloaga, comb. nov. *Streptostachys acuminata* Renvoize, Kew Bull. 39: 182. 1984. TIPO: Brasil. Bahia: estrada de Lençois, BR-242, 5 km ao N de Lençois, 19 Dec. 1981, *André M. de Carvalho, G. P. Lewis & J. L. Hage 1007 bis* (holotipo, K; fotografía del tipo y fragmento, SI).

Brachiaria tatianae Zuloaga & Soderstrom, Smithsonian Contr. Bot. 59: 7. 1985. [*Panicum megastachyum* Nees, Agrost. Bras.: 154. 1829. No *Panicum megastachyum* Nees ex Trin., 1826.] TIPO: Brasil. Minas Gerais: habitat in marginibus sylvarum Districtus Adamantum ad Tejuco etc. provinciae Minarum generalium, *Martius s.n.* (holotipo, M, fragmento, US).

Plantas perennes, con cañas multinodes de 1.80–2 m de alto, simples, erectas; entrenudos cilíndricos, ralamente pilosos hacia la porción superior a glabros; nudos pubescentes, comprimidos, castaños. Vainas de aproximadamente 15 cm de largo, pubescentes, los bordes membranáceos, aurículas reducidas, cuello piloso. Lígulas cortamente membranáceas en la base, luego largamente ciliadas, de 1.5 mm de largo. Láminas lanceoladas, de 26–40 cm de largo, 1.5 cm de ancho, planas, subcordadas, acuminadas, cortamente pilosas en ambas caras, los márgenes cartilaginosos. Inflorescencia terminal laxa, multiflora, piramidal, de 25–35 cm de largo; eje principal anguloso, pubescente, racimos aproximadamente 25, los inferiores verticilados, los superiores alternos a subopuestos, divergentes, ejes de los racimos triquetros, de 5–19 cm de largo, 0.4–0.6 mm de ancho, flexuosos, cortamente pilosos y escabrosos, terminando en una espiguilla desarrollada; axilas de las ramificaciones cortamente pilosas; espiguillas en pares, la inferior subsésil, solitarias hacia el ápice de los racimos; pedicelos triquetros, de 0.8–4 mm de largo, largamente pilosos cerca de la inserción de la espiguilla. Espiguillas largamente elipsoides, de 6–6.8 mm de largo, 2.2–2.4 mm de ancho, pilosas hacia el ápice de glumas y lemma inferior. Gluma inferior ovada, de 3.5–3.8 mm de largo, abrazadora, poco más de ½ del largo de la espiguilla, 5–7-nervia, con los nervios anastomosados hacia el ápice, separada de la gluma superior por un corto entrenudo. Gluma superior de 5.2–6.1 mm de largo, 7–9-nervia, dejando libre el ápice del antecio superior. Lemma inferior 5–7-nervia. Pálea inferior elíptica, de 4.5–5.9 mm de largo, 1.6–2.1 mm de ancho, hialina, los bordes ciliados, glabra en el resto de la superficie; flor inferior presente, lodículas 2, de 0.5 mm de largo, estambres 3, anteras purpúreas de 2.7 mm de largo. Antecio superior elipsoide, de 4.7–5.9 mm de largo, 1.6–2.1 mm de ancho, pajizo, endurecido, transversalmente rugoso, con papilas verrugosas sobre toda la superficie, lemma de ápice cortamente crestado y piloso, raquilla prolongada por encima del antecio superior en forma de un mucrón de tamaño variable; lodículas 2, conduplicadas, abrazando los bordes inferiores de la pálea, estambres 3, anteras de 3 mm de largo; estilos libres, estigmas plumosos. Cariopsis no visto.

Distribución. Conocida hasta el presente para Bahia, Brasil, creciendo en bordes de bosques.

Observaciones. Entre los caracteres más importantes de la especie se encuentran los pedicelos largamente pilosos en su porción apical, antecio superior transversalmente rugoso y con raquilla prolongada por encima de la inserción del antecio superior.

En el catálogo de colección de André M. de Carvalho figura (Mattos Silva, comm. pers.) únicamente el número 1007. Al enviarse material de este botánico en consulta a Kew, Renvoize advirtió que había mezcla dentro de dicha numeración, correspondiendo el número 1007 a *Ichnanthus bambusiflorus* (Trin.) Doell, existiendo otro especimen diferente, al que Renvoize dió el número 1007 bis y describió como *S. acuminata*. Cabe destacar que el holotipo de esta última especie se encuentra depositado en K y no en CEPEC como consta en la diagnosis original de la especie.

CARACTERES HISTOFOLIARES EN CORTE TRANSVERSAL (FIG. 4D, F)

Transcorte plano, de 130–200 μm de espesor; zonas costales e intercostales suavemente pronunciadas; costilla central no diferenciada; 7–9 haces vasculares secundarios entre haces vasculares primarios contíguos, haces primarios y secundarios en correspondencia con las zonas costales; haces vasculares adyacentes a una distancia de 150–185 μm y separados por 2–3 células clorenquimáticas. Haces vasculares primarios de contorno circular, trabados, equidistantes de ambas epidermis, rodeados por 2 vainas, la vaina interna mestomática y la vaina externa parenquimática Kranz, de 12–14 células con cloroplastos especializados de po-

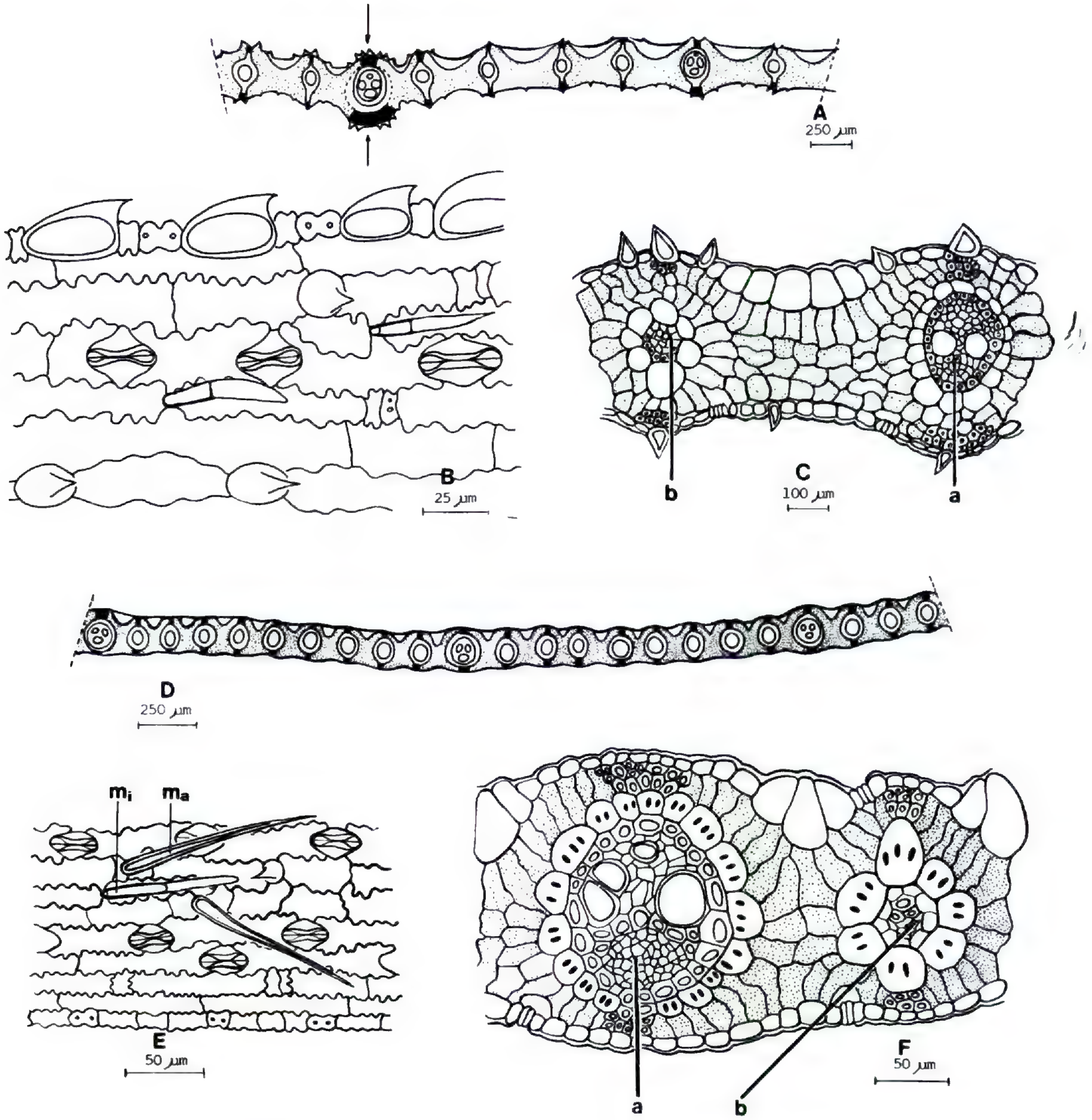

FIGURA 4. A–C. *Streptostachys robusta*.—A. Transcorte de una porción de la semilámina mostrando costilla central (flechas).—B. Detalle de la epidermis abaxial.—C. Detalle de la semilámina en transcorte, entre un haz vascular primario y secundario. D–F. *Urochloa acuminata*.—D. Transcorte de una porción de la semilámina.—E. Detalle de la epidermis abaxial.—F. Detalle de la semilámina en transcorte, entre un haz vascular primario y secundario. a, haz vascular primario; b, haz vascular secundario; ma, macropelo; mi, micropelo. (A–C de *Belem & Pinheiro 2381*; D–F de *de Carvalho et al. 1007 bis.*)

sición centrífuga (?), interrumpida hacia la cara abaxial o hacia ambas caras por tejido mecánico. Células Kranz de paredes tangenciales externas marcadamente convexas y de paredes radiales subrectas en corte transversal, y más o menos cuadradas a rectangulares en vista paradermal, con el eje mayor perpendicular; elementos del metaxilema en contacto directo con la vaina mestomática. Haces vasculares secundarios de contorno poligonal, trabados y equidistantes de ambas epidermis, vaina mestomática presente o ausente, cuando presente con pocas células adyacentes al floema; vaina Kranz contínua, compuesta por 8–11 células ± globosas; extensiones de la vaina con 1 o 2 células parenquimáticas incoloras ocasionalmente presentes hacia la cara adaxial. Clorénquima radiado alrededor de los haces vasculares en 1 capa, células tabulares, raquimorfas. Células fusoides ausentes. Células buliformes en grupos de 3 células tipo "Sporobolus," presentes en las zonas

intercostales adaxiales. Esclerénquima poco desarrollado en correspondencia con los haces vasculares y el margen foliar. Cristales ausentes. Almidón presente en las células de la vaina Kranz.

CARACTERES EPIDÉRMICOS DE LA LÁMINA EN VISTA PARADERMAL (FIG. 4E)

Zonas costales con cuerpos de sílice halteriformes; aguijones ausentes. Zonas intercostales con células largas rectangulares, alargadas longitudinalmente, más de tres veces más largas que anchas, de paredes anticlinales longitudinales onduladas; células cortas solitarias. Aparatos estomáticos subdiscoidales a romboidales de 28–33 μm de largo, 20–24 μm de ancho, distribuidos en dos hileras en las zonas intercostales. Ganchos presentes, aislados. Micropelos 2-celulares, fusiformes, de 66–100 μm de largo, célula basal más corta que la distal, de paredes gruesas, célula distal de paredes delgadas y de ápice redondeado. Macropelos unicelulares de 100–140 μm de largo, de paredes engrosadas y base bulbosa, asociada a 2 células epidérmicas no sobreelevadas, ápice agudo. Papilas ausentes.

Observaciones. Dado que para el estudio histofoliar se ha contado sólo con material de herbario, correspondiente al ejemplar tipo de *Streptostachys acuminata* y al de *Brachiaria tatianae*, no se ha podido establecer con exactitud la posición de los cloroplastos en la vaina Kranz, si bien los mismos están aparentemente dispuestos en forma centrífuga en relación al nervio.

ESPECIE DUDOSA

Como ya se ha indicado en la discusión, la posición de *S. robusta* se debe considerar dudosa, dado que el material herborizado es inmaduro.

Streptostachys robusta Renvoize, Kew Bull. 39: 182. 1984. TIPO: Brasil. Bahia: Mun. Ilheus, 16 km SW of Olivença, toward Vila Brasil, 21 May 1976, *Calderón et al. 2443* (holotipo, CEPEC*; isotipo, US).

Plantas perennes?, base no vista, hasta de 1.8 m de alto (según etiqueta); cañas con nudos inferiores con raices adventicias; entrenudos cilíndricos, huecos, glabros; nudos comprimidos, oscuros, glabros. Vainas estriadas, glabras, con los bordes membranáceos. Lígulas membranáceas. Láminas lanceoladas, de 32–40 cm de largo, 3.8–4.5 cm de ancho, con pseudopecíolo oscuro de 0.7–0.8 cm de largo, piloso en los márgenes; láminas asimétricas, escabriúsculas en ambas caras, con los bordes cartilaginosos, pilosos hacia la base, nervio medio marcado. Inflorescencia terminal laxa, amplia, hasta de 40 cm de largo; eje principal escabriúsculo, anguloso, ramificaciones inferiores verticiladas, con racimos hasta de 25 cm long., ejes de las ramificaciones escabrosos, con espiguillas en pares o sobre cortas ramificaciones de tercer orden, axilas de las ramificaciones cortamente pilosas; pedicelos cortos, triquetros, escabrosos. Espiguillas lanceoladas, de 5.5 mm de largo, 1.5 mm de ancho, comprimidas lateralmente. Gluma inferior de 5 mm de largo, ¾–⅘ del largo de la espiguilla, acuminada, 5-nervia, escabrosa en ambas caras y con largos pelos blanquecinos hacia la porción superior. Gluma superior 7-nervia, acuminada, cortamente pilosa sobre ambas caras. Lemma inferior pilosa hacia el ápice. Antecio superior con apéndices membranáceos en los bordes inferiores de la lemma.

Material adicional examinado. BRASIL. BAHIA: Margem da Rodovía Una-Olivença, 1 June 1966, *Belem & Pinheiro 2381* (CEPEC*, UB, US).

Distribución. Bahia, Brasil. Crece en suelos arenosos, es común en bordes de selvas y costados del camino.

Observaciones. Todo el material de *S. robusta* coleccionado hasta el presente es inmaduro, tal como fue indicado por Renvoize (1984) en su diagnosis original, lo cual no permite dar una descripción apropiada del antecio superior de la especie.

CARACTERES HISTOFOLIARES EN CORTE TRANSVERSAL (FIG. 4A, C)

Transcorte plano, de 230–560 μm de espesor, con zonas costales e intercostales suavemente pronunciadas; costilla central con 1 haz vascular primario asociado a células parenquimáticas incoloras; 4–6 haces vasculares secundarios entre haces vasculares primarios contíguos, haces primarios y secundarios en correspondencia con las zonas costales; haces vasculares adyacentes a una distancia de 360–520 μm y separados por 7–9 células clorenquimáticas. Haces vasculares primarios de contorno circular, trabados, rodeados por 2 vainas, una interna mestomática y una externa parenquimática sin cloroplastos especializados; vaina parenquimática contínua, compuesta por 17–21 células globosas, ocasionalmente separada del tejido mecánico por 2–4 células parenquimáticas incoloras. Haces vasculares secundarios de contorno angular, trabados; vaina parenquimática contínua de 6–9 células; vaina mestomática incompleta en correspondencia con el floema; proyecciones de la vaina con 2–4 células hacia ambas caras. Clorénquima irregularmente radiado alrededor de los ha-

ces vasculares, con células tabulares, raquimorfas, dispuestas en dos capas hacia la cara adaxial y en una capa hacia la cara abaxial; células clorenquimáticas tabulares y semejando un tejido en empalizada por debajo de las células buliformes, con cloroplastos abundantes en relación al resto del tejido clorenquimático; espacios intercelulares presentes. Células fusoides ausentes. Células buliformes presentes en las zonas intercostales adaxiales, en grupos regulares de 6–8 células dispuestas en "abanico." Esclerénquima hipodérmico, discontínuo, asociado a los haces vasculares primarios y secundarios y el margen foliar. Cristales ausentes. Amiloplastos presentes en las células clorenquimáticas.

CARACTERES EPIDÉRMICOS DE LA LÁMINA EN VISTA PARADERMAL (FIG. 4B)

Zonas costales con cuerpos de sílice halteriformes; aguijones presentes en ambas caras. Zonas intercostales con células largas rectangulares, más de tres veces más largas que anchas, de paredes onduladas; células cortas solitarias o en pares sílico-suberosos. Aparatos estomáticos romboidales, de 40–50 μm de largo, 33–40 μm de ancho, distribuidos en las zonas intercostales en 2–4 hileras. Ganchos presentes en las zonas intercostales. Micropelos 2-celulares, fusiformes, de 64–72 μm de largo, célula basal más corta que la distal, de paredes engrosadas, célula distal de paredes delgadas y ápice agudo. Macropelos no vistos. Papilas ausentes.

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A KEY TO THE GENERA OF LAURACEAE IN THE NEW WORLD[1]

Henk van der Werff[2]

ABSTRACT

A key to the twenty-nine genera of Lauraceae naturally occurring in the western hemisphere is presented. The key is based on floral and vegetative characters only. A brief statement on distribution and size of the genera is provided, together with a note on cupule shape. A Spanish translation of the key is included.

Lauraceae have, in general, the reputation of being difficult to identify. After having studied the neotropical members of this family for the last six years, I fully agree that the reputation is well deserved. There are various reasons for this. In the first place, many collections are sterile or fruiting and lack the floral characters needed for identification. To date, there are no keys for the generic identification of nonflowering specimens, and it is unlikely such a key will become available in the future. Sterile specimens may be recognized to species by a botanist familiar with the family, but if such instantaneous recognition does not occur, the specimen is likely to remain unidentified even to genus and therefore inaccessible for a long time. Fruiting specimens stand a better chance of being identified because the cupule (or its absence) contains useful information, especially when old stamens remain on the cupule. However, I am not able to construct a workable key based on fruit and vegetative characters. From a taxonomic point of view, fruiting specimens are valuable, even though difficult to identify, whereas sterile specimens are of little or no use. For botanists making forest inventories or studying species diversity, sterile voucher specimens are useful, hence collected, and end up on the desk of a specialist, where they often remain unidentified.

Even with good flowering material at hand, identification to genus is often difficult. In my opinion, the main reason for this problem is that no workable keys exist. The published keys are partly obsolete (such as Mez, 1889), are of regional scope (MacBride, 1938; Kostermans, 1936; Allen, 1945), use both floral and fruit characters (Kostermans, 1957; Hutchinson, 1964), or share a combination of these problems. Keys that are based on floral and fruit characters create special problems. As a rule, both floral and fruit characters are necessary for generic identification, but a single specimen rarely has both flowers and fruits. Typically, fruits need several months for development, by which time the flowers have long fallen off. Rarely, fruits from an earlier flowering season persist long enough to be collected with fresh flowers, but that is an exception. In such cases, flowers and fruits do not occur on the same inflorescence. Occasionally, one finds flowers and "fruits" on the same inflorescence. In my experience, such "fruits" are usually diseased and deformed. Thus, because flowering specimens almost never have fruits, a key that requires both flowers and fruits is not workable and will frustrate its user. However, it is possible to construct a generic key for neotropical Lauraceae based solely on floral and vegetative characters. I present such a key below, which includes all American genera.

The most important floral characters used in this key, as well as in earlier keys, are number of stamens, number of anther cells per stamen, sexual condition of the flowers, and tepals equal or unequal. These characters, although readily visible, are often variable within a genus, and this variation has rarely been incorporated in earlier keys. For example, *Persea* is usually presented as having nine 4-celled stamens, whereas the neotropical species can have nine or six stamens, these being all 4-celled, all 2-celled, or some 4- and some 2-celled. Moreover, the tepals can be equal or unequal and

[1] A. Gentry, M. Grayum, J. Rohwer, and W. D. Stevens critically read the manuscript and suggested improvement. W. D. Stevens kindly translated the key into Spanish. J. Myers made the illustrations.

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deciduous or persistent in fruit. In order to accommodate these permutations of characters, it is at times necessary to have a genus appear several times in the key.

While constructing this key, I have completely ignored any phylogenetic relationships among the genera, mainly because phylogenetic schemes of Lauraceae are partially based on fruit characters (Kostermans, 1957) or are based on wood and bark anatomy (Richter, 1981). These supposedly phylogenetic classifications (which are quite different from each other) cannot readily be followed in the construction of a key based on floral characters. Instead, my aim is to provide a workable key for the identification of flowering Lauraceae.

Before presenting the key, I will briefly describe the flower structure of Lauraceae. Examples are based on American genera, and unusual conditions of palaeotropical genera (such as dimerous flowers in *Potameia*) are not discussed. Typically, each flower has two whorls of three tepals each. The whorls are usually equal in size and shape, but there are exceptions. Tepals are unequal in all species of *Caryodaphnopsis*, in many species of *Persea* (Fig. 1c), in *Anaueria*, and in a few species of *Aniba* and *Licaria*. When tepals are unequal, the outer three are smaller, except in *Licaria*, where the outer three tepals can be larger (Fig. 1d). "*Chlorocardium*" is unusual in having the tepals in whorls of four or irregular. The stamens are arranged in four whorls of three each (with the exception of "*Chlorocardium*," which has stamens in whorls of four) and are opposite the tepals. The whorls are counted from the outside to the center of the flower. Whorl I is opposite the outer tepals, whorl II is facing the inner tepals, whorl III is opposite whorl I, and whorl IV opposite whorl II. With the exception of *Litsea* and "*Chlorocardium*," whorl IV is always staminodial or lacking. The stamens of whorl III nearly always have two globose glands at their base, the exceptions being *Mezilaurus* and *Williamodendron*, in which these glands are absent. In *Phyllostemonodaphne* and *Urbanodendron* all stamens have glands at their base. In *Pleurothyrium* the glands are strongly enlarged and may become fused, completely surrounding all stamens. In general, the stamens of whorls I and II are (nearly) identical and seemingly form one whorl of six stamens. The exceptions are *Dicypellium* and *Phyllostemonodaphne*, where the stamens of whorl I have become tepaloid and sterile, with only whorl II and III fertile. Stamens of whorl III differ occasionally from those of whorls I and II in number of anther cells. If different, whorl III has usually fewer anther cells (whorls I and II 4-celled, III 2-celled or sterile; whorls I and II 2-celled, whorl III sterile), but *Endlicheria anomala* has whorls I and II 2-celled and whorl III 4-celled. A further variation is that any of whorls I, II, and III can be sterile. (In some species only whorl I is fertile, or only I and II are fertile, or II and III are fertile, or only III is fertile; I have not yet seen a species with only whorl II fertile.) Table 1 presents the various androecial combinations and their distributions among neotropical Lauraceae, "*Gamanthera*" excluded. If a key were to include all known combinations of number of stamens, their position and number of anther cells in each whorl, one would end up with a very long and tedious (but workable) key. However, I found that a shorter and more practical key can be made by excluding the condition of the stamens of whorl III, as has first been done by Mez (1889). Exceptional species or groups of species, such as the 2-celled species of *Persea* and *Caryodaphnopsis* and the *Aiouea* species with three stamens are keyed out separately.

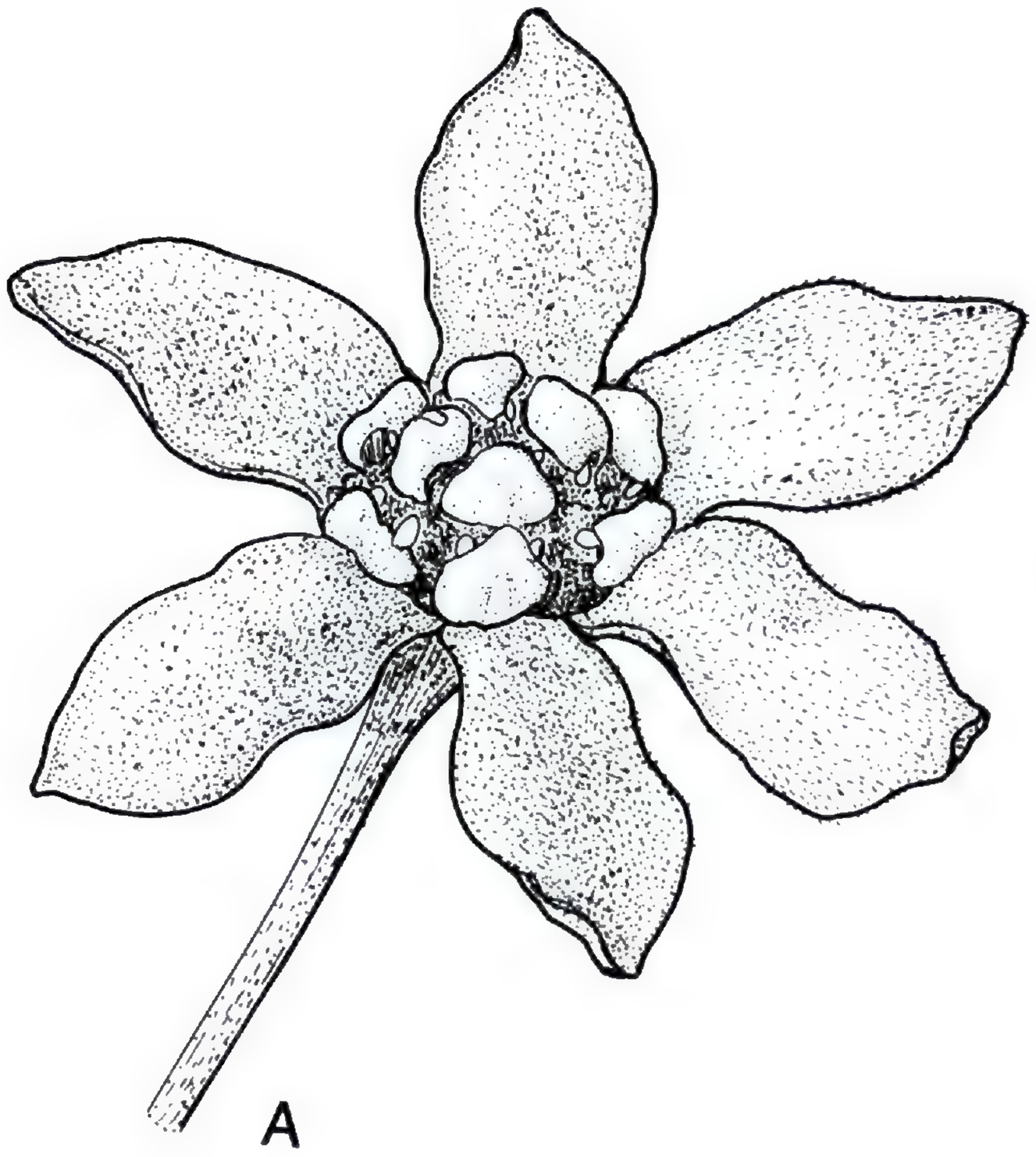
Following the key, the distribution, approximate number of species and fruit type are briefly described. When an unusual leaf position occurs in a genus, this is also mentioned.

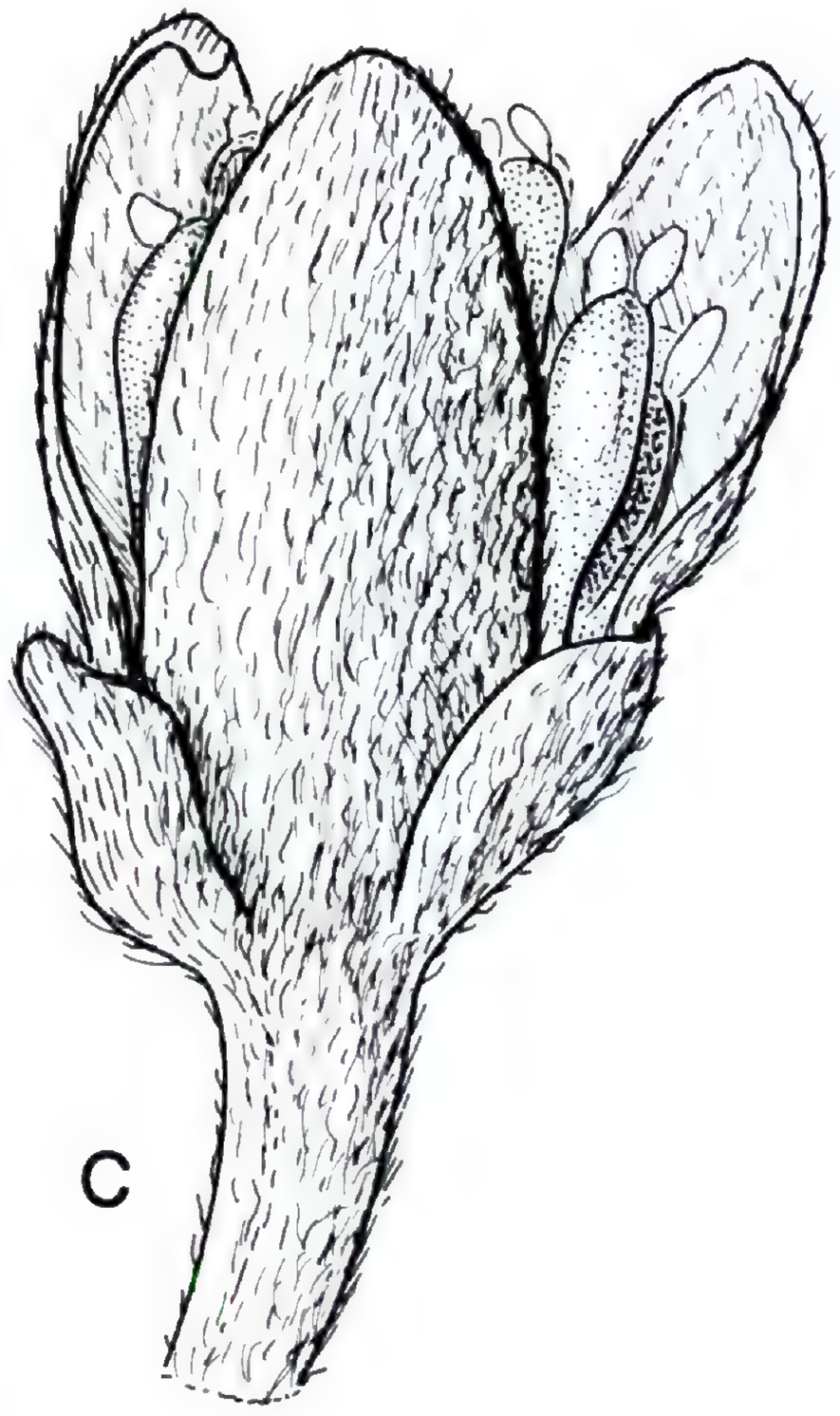
A good magnifying glass, or preferably a dissecting microscope, is a necessity for identifying Lauraceae.

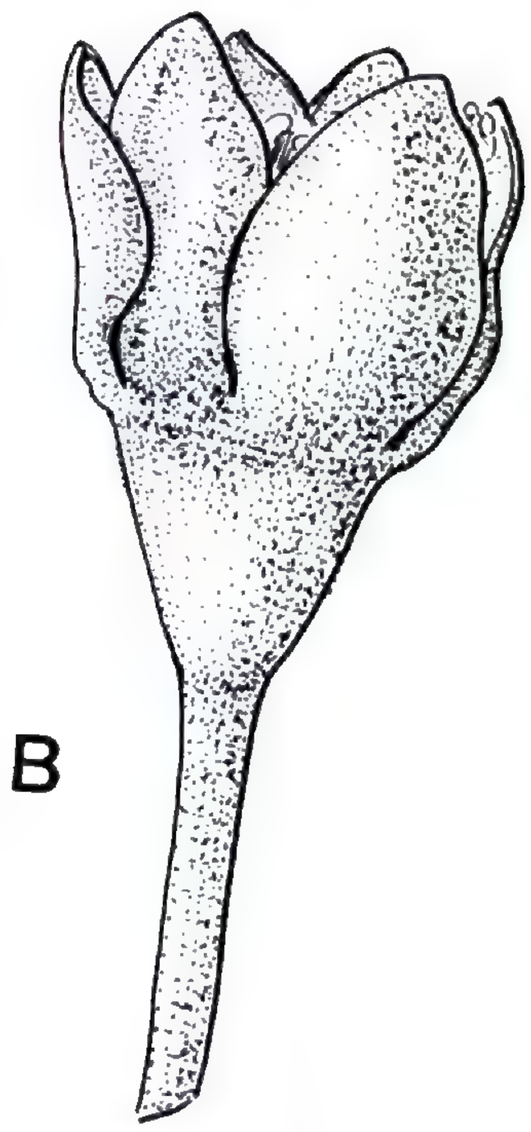
Included in the key are several taxa which are not yet published ("*Chlorocardium*," "*Gamanthera*," and "*Paraia*"). Their inclusion in the key is absolutely not intended as their publication, but is done to prevent the key from being obsolete at the moment of publication.

Key to New World Genera of Lauraceae

1	Parasitic leafless vine	*Cassytha*
1	Shrubs or trees with green leaves	2
2(1)	"Stamen" 1, by complete fusion of 3 stamens	"*Gamanthera*"
2	Stamens more than 1	3
3(2)	Flowers bisexual or staminate	4
3	Flowers pistillate	42
4(3)	Stamens 3	5
4	Stamens more than 3	8
5(4)	Stamens with 4 anther cells	*Williamodendron*
5	Stamens with 2 anther cells	6
6(5)	Leaves clustered near tips of branches; anther cells extrorse; inflorescence a panicle, ultimate divisions racemose	*Mezilaurus*
6	Leaves not clustered, but alternate or opposite; position of anther cells variable (in *L. cannella* leaves somewhat clustered, but anther cells introrse); inflorescence paniculiform, ultimate division cymose	7
7(6)	Only stamens of Whorl I fertile, the cells	







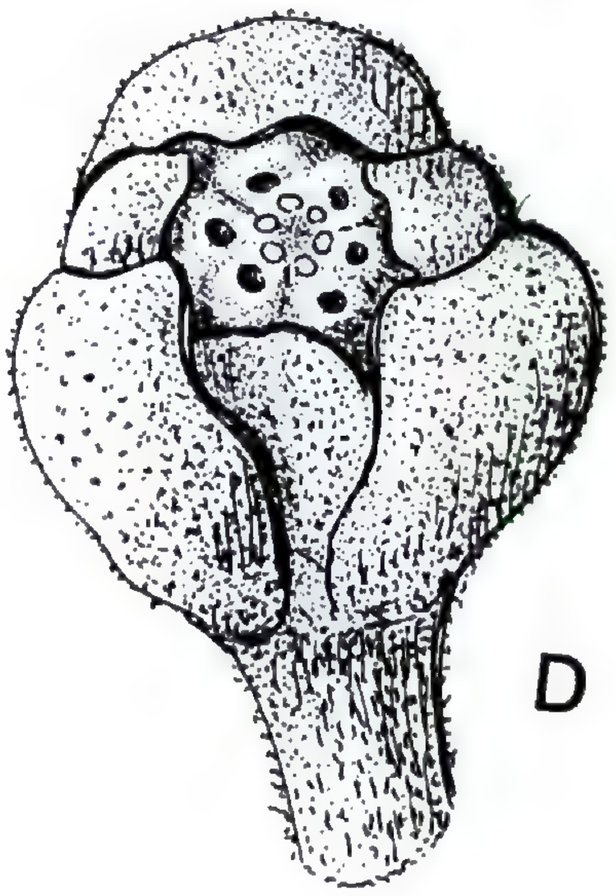


FIGURE 1. Flowers of:—A. *Nectandra grandiflora* Nees (*Gentry et al. 59163*);—B. *Ocotea atirrensis* Mez & Donn. Smith (*Grayum 6888*);—C. *Persea liebmannii* Mez (*Ishiki 1614*);—D. *Licaria bracteata* van der Werff (*Kunkel 56*).

	lateral and large, or lateral basal and small; inflorescences and flowers glabrous ..... *Aiouea*	9(8)	Flowers unisexual 10
7	Only stamens of Whorl III fertile, the cells extrorse, introrse or ± apical, not lateral; inflorescences and/or flowers usually with varying amounts of pubescence ..... *Licaria*	9	Flowers bisexual 11
		10(9)	Leaves deciduous in winter; flowers appearing before leaves ..... *Lindera*
		10	Plants evergreen, flowers and leaves present at the same time ..... *Endlicheria*
8(4)	Outer 6 stamens each with 2 anther cells 9	11(9)	Leaves opposite 12
8	Outer 6 stamens each with 4 anther cells 23	11	Leaves alternate or clustered 15

TABLE 1. Androecial configurations of American Lauraceae.

Whorls I, II, & III 4-celled: *Caryodaphnopsis* pro parte, *Chlorocardium*, *Cinnamomum* pro parte, *Litsea*, *Nectandra*, *Ocotea*, *Paraia*, *Persea* pro parte, *Pleurothyrium*, *Povedodaphne*, *Rhodostemonodaphne*, *Sassafras*, *Umbellularia*, *Urbanodendron* pro parte

Whorls I, II, & III 2-celled: *Aiouea* pro parte, *Aniba* pro parte, *Beilschmiedia*, *Caryodaphnopsis* pro parte, *Cassytha*, *Cryptocarya*, *Endlicheria* pro parte, *Kubitzkia* pro parte, *Lindera*, *Persea* pro parte, *Urbanodendron* pro parte

Whorls I & II 4-celled, III 2-celled: *Cinnamomum* pro parte, *Kubitzkia* pro parte, *Persea* pro parte

Whorls I & II 4-celled, III 0-celled: *Persea* pro parte

Whorls I & II 2-celled, III 4-celled; *Endlicheria anomala*

Whorls I & II 2-celled, III 0-celled: *Aiouea* pro parte, *Anaueria*, *Aniba* pro parte, *Caryodaphnopsis* pro parte

Whorl I 2-celled, II & III 0-celled: *Aiouea* pro parte

Whorl I 0-celled, II & III 4-celled; *Dicypellium*

Whorl I 0-celled, II & III 2-celled: *Phyllostemonodaphne*

Whorl I & II 0-celled, III 4-celled: *Williamodendron*

Whorl I & II 0-celled, III 2-celled: *Licaria*, *Mezilaurus*

12(11) Stamens 6, triangular, dark red, the filaments wider than the anthers, united at the base; outer tepals about ½ as long as the inner ones ..... *Anaueria*

12 Stamens 6 or 9, filaments free, narrower than the anthers; stamens never dark red; tepals equal or strongly unequal, outer ones ≤¼ the size of inner ones 13

13(12) Outer tepals ≤¼ the size of inner tepals ..... *Caryodaphnopsis*

13 Tepals equal 14

14(13) Floral tube deep, about as long as the tepals ..... *Cryptocarya*

14 Floral tube shallow, much shorter than the tepals ..... *Beilschmiedia*

15(11) Filaments of stamens of Whorl III united; flowers red ..... *Kubitzkia*

15 Filaments free; flower color variable, including red in some species 16

16(15) Stamens of Whorl I sterile, tepaloid; fertile stamens 6, representing Whorls II and III ..... *Phyllostemonodaphne*

16 Stamens of Whorl I fertile; fertile stamens 9 or 6; if 6, representing Whorl I and II 17

17(16) Fertile stamens 9, each with 2 glands at the base ..... *Urbanodendron*

17 Fertile stamens 6 or 9, only those of Whorl III with glands at their base 18

18(17) Outer tepals ca. ½ as long as inner ones (Fig. 1c) 19

18 Tepals equal or nearly so (Fig. 1a and b) 20

19(18) Staminodia (whorl IV) well developed, with sagittate or cordate apices; floral tube very short, much shorter than tepals; Andean species, 1,000–2,500 m elev. ..... *Persea*

19 Staminodia (whorl IV) lacking; floral tube well developed; lowland Amazonian species ..... *Aniba canelilla* or *A. parviflora*

20(18) Floral tube very shallow, scarcely visible at anthesis ..... *Beilschmiedia*

20 Floral tube well developed, about as long as the tepals 21

21(20) Leaves with a fine, raised reticulation; floral tube deep and narrow, the tepals ± spreading and flowers clearly wider than floral tube; filaments much narrower than anthers; staminodia well developed ..... *Cryptocarya*

21 Leaves with lax reticulation or this not ap-

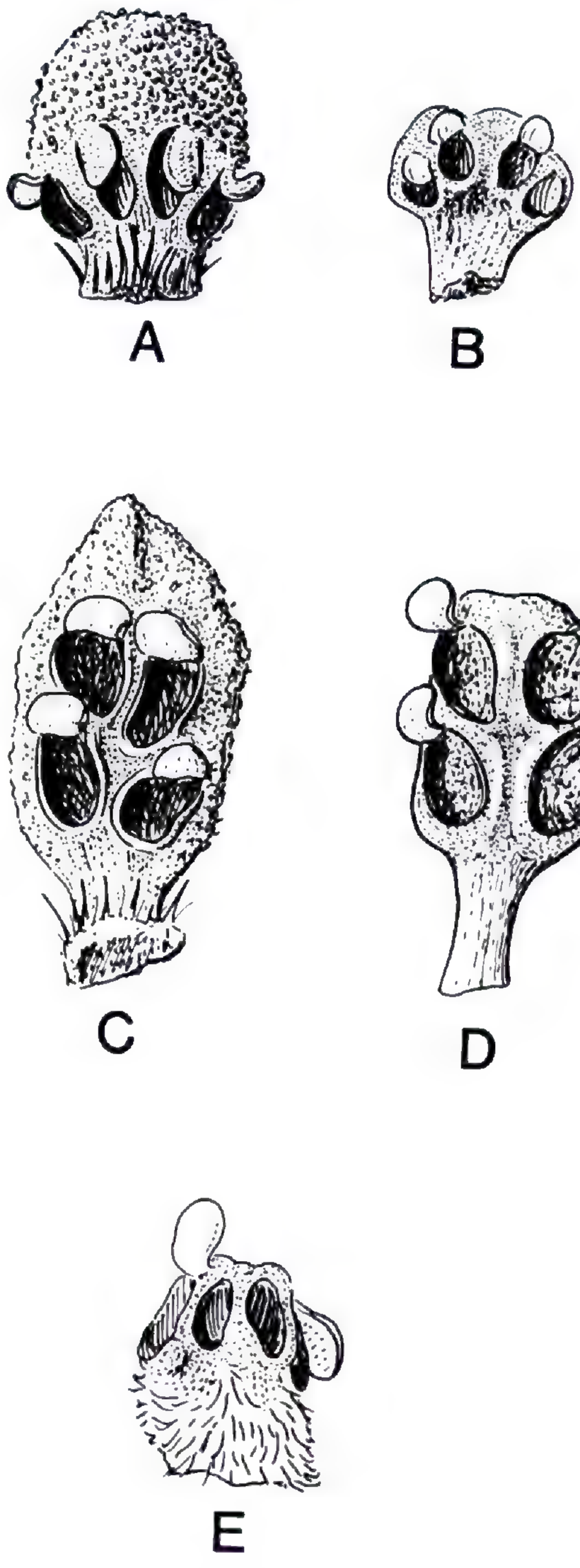


FIGURE 2. Stamens (whorl I or II) of:—A. *Nectandra reticulata* (R. & P.) Mez (*Kayap 161*);—B. *Nectandra membranacea* (Sw.) Griseb. (*Cuadros 2839*);—C. *Ocotea veraguensis* (Meissner) Mez (*Stevens 6476*);—D. *Ocotea pulchella* Mart. (*Goetzke 210*);—E. *Rhodostemonodaphne kunthiana* (Nees) Rohwer (*Perry s.n.*).

parent; floral tube shallow or deep; if deep, tepals erect and flowers about as wide as floral tube; filaments frequently poorly differentiated from anthers; staminodia present or absent 22

22(21) Flowers (minutely) tomentellous, tomentose or with appressed pubescence, but never pruinose; filaments of stamens usually densely pubescent, poorly differentiated from anthers; leaves alternate or clustered ..... *Aniba*

22 Flowers usually glabrous, infrequently with scattered hairs, sometimes pruinose; filaments of stamens usually glabrous and differentiated from anthers; leaves alternate ..... *Aiouea*

23(8) Flowers unisexual 24

23 Flowers bisexual 27

24(23) Young inflorescences enclosed in decussate bracts; flowers arranged in pseudo-umbels ..... *Litsea*

24 Young inflorescences not enclosed in decussate bracts; flowers arranged in panicles or racemes 25

25(24) Deciduous trees; flowers appearing before or with young leaves, leaves often lobed ..... *Sassafras*

25 Evergreen plants with mature leaves when flowering; leaves never lobed 26

26(25) Anther cells arranged in a low arch (Fig. 2e); anthers poorly differentiated from filaments ..... *Rhodostemonodaphne*

26 Anther cells arranged in 2 rows (Fig. 2c and d); anthers clearly differentiated from the much narrower filament (rarely filaments very short) ..... *Ocotea*

27(23) Flowers arranged in pseudo-umbel, this, when young, covered by bracts ..... *Umbellularia*

27 Flowers arranged in paniculiform inflorescences, these never enclosed by bracts 28

28(27) Leaves opposite 29

28 Leaves alternate or whorled 31

29(28) Outer tepals ≤ ¼ the size of the inner ones; leaves often strongly triveined ..... *Caryodaphnopsis*

29 Tepals equal; leaves pinnately veined 30

30(29) Stamens 12 or more; leaves glabrous or nearly so on lower surface ..... "*Chlorocardium*"

30 Stamens 9; leaves ferruginous tomentose or tomentellous on lower surface ..... *Nectandra oppositifolia*

31(28) Anther cells on the flat tip of columnar stamens ..... *Povedadaphne*

31 Anther cells not apical; stamens not columnar 32

32(31) All stamens with 2 glands at their base, the glands free ..... *Urbanodendron*

32 Only stamens of Whorl III with glands (in *Pleurothyrium* glands greatly enlarged and sometimes fused) 33

33(32) Stamens of Whorl III with fused filaments; flowers red ..... *Kubitzkia*

33 Stamens of Whorl III with free filaments; if filaments seemingly fused (in some *Ocotea* species), then flowers white to yellow, never red 34

34(33) Stamens of Whorl I devoid of anther cells, tepaloid ..... *Dicypellium*

34 Stamens of Whorl I fertile, not tepaloid 35

35(34) Outer tepals about ½ the size of the inner ones 36

35 Tepals equal or nearly so 37

36(35) Stamens of Whorls I and II with a sterile, triangular tip; leaf apex rounded or obtuse; leaves whorled; Guyanas and adjacent Brazil and Venezuela ..... *Ocotea rubra*

36 Stamens of Whorls I and II without a sterile, triangular tip, the anther cells occupying the entire anther; leaf apex various; leaves alternate or whorled; widespread, from SE U.S.A. to Brazil and Chile ..... *Persea*

37(35) Staminal glands greatly enlarged, protruding between the outer 6 stamens and sometimes fused into a large, pillowlike mass; stamens of Whorls I and II with at least 2 lateral anther cells ..... *Pleurothyrium*

37 Staminal glands not enlarged, not protruding between outer stamens; free; outer stamens with introrse cells 38

38(37) Staminodia representing Whorl IV well developed, with a cordate or sagittate apex; filaments of stamens as long as anthers or longer 39

38 Staminodia representing Whorl IV small or lacking; if present, mostly without a cordate or sagittate tip; filaments of stamens shorter than or as long as anthers (a few species of *Ocotea* have large staminodia with a cordate tip, but these have stamens with a very short filament) 40

39(38) Leaves usually tripliveined, alternate, frequently tufts of hairs present in the axils of the lowermost veins ..... *Cinnamomum*

39 Leaves pinnately veined, alternate or clustered; axillary tufts of hairs lacking ..... *Persea*

40(38) Leaves clustered; twigs with clusters of scars from fallen bracts; tepals roundish, hyaline, with a pubescent base, otherwise glabrous ..... "*Paraia*"

40 Leaves alternate; twigs without clusters of scars from fallen bracts; tepals not roundish, not hyaline, glabrous or with different distribution of pubescence 41

41(40) Anther cells arranged in 2 vertical rows (Fig. 2c and d); stamens and inner face of tepals glabrous or variously pubescent, rarely papillose (if papillose, the anther cells clearly in 2 vertical rows); tepals free at base, falling individually in old flowers; a few old stamens sometimes present on cupule of young fruits; tepals at anthesis erect (Fig. 1b) or spreading ..... *Ocotea*

41 Anther cells arranged in an arc (Fig. 2a and b); stamens and inner face of tepals papillose; tepals united at the base, usually falling as a unit (together with stamens) in old flowers; stamens rarely present on cupule of young fruits; tepals at anthesis spreading (Fig. 1a) ..... *Nectandra*

42(3) Plants cold-season deciduous and/or inflorescences subumbellate and young flowers enclosed in involucrate bracts 43

42 Plants evergreen and inflorescences paniculate, the flowers not enclosed in involucrate bracts 45

43(42) Inflorescences racemose or paniculate; leaves often trilobed ..... *Sassafras*
43 Inflorescences subumbellate; leaves never trilobed 44
44(43) Plants deciduous; pseudo-umbels sessile or nearly so ..... *Lindera*
44 Plants deciduous or evergreen; pseudo-umbels pedunculate ..... *Litsea*
45(42) Staminodes straplike, the filaments about as wide as the anther; traces of locelli four on each anther ..... *Rhodostemonodaphne*
45 Staminodes club-shaped, the filaments narrower than the anthers 46
46(45) Anthers with 4 remnants of locelli; leaves alternate ..... *Ocotea*
46 Anthers with 2 remnants of locelli; leaves alternate or whorled ..... *Endlicheria*

Clave Para los Géneros de Lauraceae del Nuevo Mundo

1 Trepadoras parásitas y áfilas ..... *Cassytha*
1 Arbustos o árboles con hojas verdes 2
2(1) Estambre aparentemente 1 por fusión completa de 3 estambres ..... "*Gamanthera*"
2 Estambres claramente más de 1 3
3(2) Flores bisexuales o estaminadas 4
3 Flores pistiladas 42
4(3) Estambres 3 5
4 Estambres más de 3 8
5(4) Anteras con 4 tecas ..... *Williamodendron*
5 Anteras con 2 tecas 6
6(5) Hojas agrupadas en los extremos de las ramas; tecas extrorsas; inflorescencia una panícula con las divisiones últimas racemosas ..... *Mezilaurus*
6 Hojas alternas u opuestas, no agrupadas; orientación de las tecas variable (en *L. cannella* hojas algo agrupadas, pero entonces las tecas introrsas); inflorescencia paniculiforme, divisiones últimas cimosas 7
7(6) Solamente los estambres del Verticilo I fértiles, tecas laterales y grandes o lateral-basales y pequeñas; inflorescencias y flores glabras ..... *Aiouea*
7 Solamente los estambres del Verticilo III fértiles, tecas extrorsas, introrsas o ±apicales, nunca laterales; inflorescencias y/o flores usualmente pubescentes ..... *Licaria*
8(4) Anteras de los 6 estambres exteriores con 2 tecas 9
8 Anteras de los 6 estambres exteriores con 4 tecas 23
9(8) Flores unisexuales 10
9 Flores bisexuales 11
10(9) Hojas deciduas en el invierno, flores producidas antes que las hojas ..... *Lindera*
10 Hojas no deciduas, flores y hojas presentes a la vez ..... *Endlicheria*
11(9) Hojas opuestas 12
11 Hojas alternas o agrupadas 15
12(11) Estambres 6, rojo-obscuros, con filamentos más anchos que las anteras y unidos en la base; tépalos exteriores cerca de ½ del largo de los interiores ..... *Anaueria*
12 Estambres 6 o 9, nunca rojo-obscuros, con filamentos más delgados que las anteras y libres; tépalos iguales o muy desiguales con los exteriores ¼ o menos del largo de los interiores 13
13(12) Tépalos exteriores ¼ o menos del largo de los interiores ..... *Caryodaphnopsis*
13 Tépalos iguales 14
14(13) Tubo floral profundo, tan largo como los tépalos ..... *Cryptocarya*
14 Tubo floral poco profundo, mucho más corto que los tépalos ..... *Beilschmiedia*
15(11) Estambres del Verticilo III con filamentos unidos; flores rojas ..... *Kubitzkia*
15 Estambres con filamentos libres; flores raramente rojas 16
16(15) Estambres del Verticilo I estériles, tepaloides; estambres fértiles 6, representando los Verticilos II y III ..... *Phyllostemonodaphne*
16 Estambres del Verticilo I fértiles; estambres fértiles 9 ó 6, si 6 entonces representando los Verticilos I y II 17
17(16) Estambres fértiles 9, cada uno con 2 glándulas en la base ..... *Urbanodendron*
17 Estambres fértiles 6 ó 9, solo los del Verticilo III con glándulas en la base 18
18(17) Tépalos exteriores cerca de ½ del largo de los interiores (Fig. 1c) 19
18 Tépalos iguales o casi iguales (Fig. 1a y b) 20
19(18) Estaminodios bien desarrollados, con ápices sagitados o cordados; tubo floral muy corto, mucho más corto que los tépalos; especies andinas de 1,000–2,500 msnm ..... *Persea*
19 Estaminodios ausentes; tubo floral bien desarrollados; especies amazonicas de elevaciones bajas ..... *Aniba canelilla* o *A. parviflora*
20(18) Tubo floral poco profundo, escasamente visible en la ántesis ..... *Beilschmiedia*
20 Tubo floral bien desarrollado, más o menos del mismo largo que los tépalos 21
21(20) Hojas con una reticulación fina y prominente; tubo floral profundo y angosto, tépalos ± patentes y el limbo claramente más ancho que el tubo; filamentos mucho más angostos que las anteras; estaminodios bien desarrollados ..... *Cryptocarya*
21 Hojas con una reticulación laxa o inconspicua; tubo floral poco profundo o profundo, si profundo entonces los tépalos erectos y el limbo tan ancho como el tubo; filamentos frecuentemente poco diferenciados de las anteras; estaminodios presentes o ausentes 22
22(21) Flores menudamente tomentosas o aplicado-pubescentes, nunca pruinosas; filamentos con frecuencia densamente pubescentes, poco diferenciados de las anteras; hojas alternas o agrupadas ..... *Aniba*
22 Flores usualmente glabras, infrecuentemente con tricomas dispersas, a veces pruinosas; filamentos usualmente glabros y diferenciados de las anteras; hojas alternas ..... *Aiouea*
23(8) Flores unisexuales 24
23 Flores bisexuales 27

24(23) Inflorescencias jóvenes envueltas en brácteas decusadas; flores en pseudo-umbelas ... *Litsea*

24 Inflorescencias jóvenes no envueltas en brácteas decusadas; flores en panículas o racimos ... 25

25(24) Arboles deciduos, flores producidas antes o junto con las hojas; hojas frecuentemente lobadas ... *Sassafras*

25 Arboles o arbustos perennifolios, flores producidas con las hojas maduras; hojas nunca lobadas ... 26

26(25) Tecas dispuestas en un arco bajo; anteras poco diferenciadas de los filamentos (Fig. 2e) ... *Rhodostemonodaphne*

26 Tecas dispuestas en 2 hileras; anteras claramente más anchas que los filamentos (raramente filamentos muy cortos) (Fig. 2c y d) ... *Ocotea*

27(23) Flores en pseudo-umbelas, éstas cubiertas por brácteas cuando jóvenes ... *Umbellularia*

27 Flores en inflorescencias paniculiformes, éstas nunca envueltas por brácteas ... 28

28(27) Hojas opuestas ... 29

28 Hojas alternas o verticiladas ... 31

29(28) Tépalos exteriores ¼ del tamaño de los interiores o más pequeños; hojas con frecuencia fuertemente trinervias ... *Caryodaphnopsis*

29 Tépalos iguales; hojas pinnatinervias ... 30

30(29) Estambres 12 o más; hojas glabras o casi glabras en el envés ... "*Chlorocardium*"

30 Estambres 9; hojas ferrugíneo-tomentosas en el envés ... *Nectandra oppositifolia*

31(28) Tecas en el ápice plano de los estambres columnares ... *Povedadaphne*

31 Tecas no apicales, estambres no columnares ... 32

32(31) Todo los estambres con 2 glándulas en la base, las glándulas libres ... *Urbanodendron*

32 Solamente los estambres del Verticilo III con glándulas (en *Pleurothyrium* las glándulas muy agrandadas y a veces fusionadas) ... 33

33(32) Estambres del Verticilo III con filamentos fusionados; flores rojas ... *Kubitzkia*

33 Estambres del Verticilo III con filamentos libres, o si aparentemente fusionados (en algunas especies de *Ocotea*), entonces las flores blancas a amarillas, nunca rojas ... 34

34(33) Estambres del Verticilo I estériles y tepaloides ... *Dicypellium*

34 Estambres del Verticilo I fértiles y no tepaloides ... 35

35(34) Tépalos exteriores cerca de ½ del tamaño de los interiores ... 36

35 Tépalos iguales o casi iguales ... 37

36(35) Estambres de los Verticilos I y II con ápices triangulares y estériles; hojas con ápices redondeados u obtusos; Guayanas y áreas adyacentes de Brasil y Venezuela ... *Ocotea rubra*

36 Estambres de Verticilos I y II sin ápices triangulares y estériles, las tecas ocupando toda la antera; hojas raramente con ápices redondeados u obtusos; ampliamente distribuida desde el sur de los Estados Unidos hasta Brasil y Chile ... *Persea*

37(35) Glándulas estaminales muy agrandadas, empujando entre los 6 estambres exteriores y a veces fusionadas en una masa grande como almohada; estambres de los Verticilos I y II con al menos 2 de las tecas laterales ... *Pleurothyrium*

37 Glándulas estaminales no agrandadas ni fusionadas; estambres exteriores con todas las tecas introrsas ... 38

38(37) Estaminodios representando el Verticilo IV bien desarrollados, con ápices cordados o sagitados; filamentos iguales o más largos que las anteras ... 39

38 Estaminodios representando Verticilo IV ausentes o si presentes pequeños y mayormente sin ápices cordados o sagitados; filamentos iguales o más cortos que las anteras (unas pocas especies de *Ocotea* tienen estaminodios grandes con ápices cordados, pero estas tienen filamentos muy cortos) ... 40

39(38) Hojas usualmente trinervias, alternas, frecuentemente con fascículos de tricomas presentes en las axilas de los nervios basales ... *Cinnamomum*

39 Hojas pinnatinervias, alternas o agrupadas, sin fascículos de tricomas axilares ... *Persea*

40(38) Hojas agrupadas; ramitas con fascículos de cicatrices de brácteas caídas; tépalos algo redondos, hialinos, pubescentes solamente en la base ... "*Paraia*"

40 Hojas alternas; ramitas sin fascículos de cicatrices; tépalos ni redondos ni hialinos, glabros o con la pubescencia distribuida de otra forma ... 41

41(40) Tecas dispuestas en 2 hileras (Fig. 2c y d); estambres y caras adaxiales de los tépalos glabros o variadamente pubescentes, raramente papilosos (si papilosos, las tecas claramente en 2 hileras); tépalos libres en la base y cayéndose individualmente; unos pocos estambres viejos frecuentemente presentes en la cúpula de los frutos jóvenes; tépalos erectos o patentes en la ántesis (Fig. 2b) ... *Ocotea*

41 Tecas dispuestas en un arco (Fig. 2a y b); estambres y caras adaxiales de los tépalos papilosas; tépalos unidos apenas en la base, usualmente cayéndose juntos (y juntos con los estambres); estambres raramente presentes en la cúpula de los frutos jóvenes; tépalos patentes en la ántesis (Fig. 1a) ... *Nectandra*

42(3) Plantas deciduas en el invierno y/o inflorescencias subumbeladas y flores jóvenes envueltas por brácteas involucrales ... 43

42 Plantas perennifolias con inflorescencias paniculadas, flores no envueltas por brácteas involucrales ... 45

43(42) Inflorescencias racemosas o paniculadas; hojas frecuentemente trilobadas ... *Sassafras*

43 Inflorescencias subumbeladas; hojas nunca trilobadas ... 44

44(43) Plantas deciduas; pseudo-umbelas sésiles o casi sésiles ... *Lindera*

44 Plantas deciduas o perennifolias; pseudo-umbelas pedunculadas ... *Litsea*

45(42) Estaminodios ligulados, filamentos igual de

ancho que las anteras, cada antera con vestigios de 4 tecas ..... *Rhodostemonodaphne*

45 Estaminodios claviformes, filamentos más delgados que las anteras 46

46(45) Anteras de los estaminodios con vestigios de 4 tecas; hojas alternas ..... *Ocotea*

46 Anteras de los estaminodios con vestigios de 2 tecas; hojas alternas o verticiladas ..... *Endlicheria*

Aiouea Aublet

Probably a polyphyletic genus in the currently accepted sense, as has been noted by several authors (Burger, 1988; Rohwer et al., in press; van der Werff, 1987b, 1988). The genus has been monographed by Renner (1982) and consists of about 20 species, ranging from southern Mexico to southern Brazil and Paraguay. Most species have the fruit seated on a shallow cupule with a thickened pedicel.

Anaueria Kostermans

A monotypic genus known from Amazonian forests near the border of Brazil and Peru. The seeds are said to be edible after roasting. A cupule is lacking in fruit. Flowers have green tepals and dark red stamens, very unusual in Lauraceae.

Aniba Aublet

Recently revised by Kubitzki (1982). *Aniba* includes 40–50 species, many with pleasantly aromatic yellow wood (rosewood oil is distilled from *Aniba rosaeodora*). It is distributed from Costa Rica to southern Brazil and Bolivia. Most species occur in the lowlands, but it has also been collected in the Andes up to 1,800 m. The fruit is seated in a rather deep cupule, which is often lenticellate or warty. Several species have clustered leaves.

Beilschmiedia Nees

In the Neotropics a poorly understood genus with 10–20 species, last revised by Kostermans (1938), who accepted 15 species. It has been collected from Mexico to southern Brazil and in the West Indies. The fruit lacks a cupule. In the Palaeotropics, *Beilschmiedia* is equally poorly understood, but is represented by many more species.

Caryodaphnopsis Airy Shaw

Only recently reported from the Neotropics (van der Werff & Richter, 1985), this genus includes five published neotropical species, with several more awaiting publication. The strongly unequal tepals and opposite leaves are diagnostic. Fruits (in neotropical species) are round or pearshaped, and seated on a naked pedicel. It occurs in lowland forests from Costa Rica to Peru and Brazil. The seven palaeotropical species occur in Indochina, with one species extending to New Guinea (Kostermans, 1974).

Cassytha L.

One species in the Neotropics, from Mexico to Brazil, often found near the coast, but also locally common in *Mauritia* swamps. More species occur in Australia and South Africa. The genus has been placed in its own family because of its parasitic habit, but is here retained in the Lauraceae.

"*Chlorocardium*"

A genus with two species, one from Guyana and Surinam, the other from Amazonian Ecuador and adjacent Colombia, previously included in *Ocotea*, but differing in characters of flowers, wood, and leaf position. The Ecuadorian/Colombian species is incompletely known. Fruits are described as large (to 7 × 5 cm), with a normal or very large cupule.

Cinnamomum Schaeffer

A large, poorly understood genus occurring in Asia, Australia, and the Americas. Possibly with more than 50 species in the Neotropics, known from Mexico and the West Indies to southern Brazil and Paraguay. The fruit is subtended by a small cupule, this often crowned with persistent tepals. The neotropical species have often been treated in *Phoebe*, but seem better placed in *Cinnamomum*. Many Asian species, including *C. verum*, which yields cinnamon, have opposite leaves, but all neotropical species have alternate, mostly tripliveined leaves. *Cinnamomum*, as accepted here, is possibly polyphyletic.

Cryptocarya R. Brown

A large, poorly understood pantropical genus, with ten or fewer neotropical species, mostly in southern Brazil and Chile, but also known from French Guyana and adjacent Brazil, Andean Venezuela, Ecuador, and Peru. The fruit is almost completely enclosed in the cupule, which has only a small, apical pore.

Dicypellium Nees & Martius

A small genus of two rarely collected species, restricted to Amazonian Brazil, reviewed by Rohwer (1988). The cupule is cupshaped, and has a double margin. The tepals are persistent in fruit. One species, *Dicypellium caryophyllaceum*, has been heavily exploited because of its aromatic bark.

Endlicheria Nees

A neotropical genus of about 40 species, reported from Costa Rica, the Lesser Antilles south to Paraguay, and southern Brazil. The genus is polyphyletic (Rohwer et al., in press). The cupule is variable; most species have a thick, fleshy and smooth cupule. Several species have whorled leaves.

"*Gamanthera*"

A monotypic genus recently discovered in Costa Rica, characterized by the presence of only one "stamen," actually a synandrium formed by complete fusion of three stamens (Endress, pers. comm.). The number of locelli of the synandrium can be 3, 2, or 1. The cupule is rather deeply cupshaped, with a double margin and persistent, reflexed tepals. The only species is monoecious.

Kubitzkia van der Werff

A neotropical genus of one, possibly two, species, known from Guyana, Surinam, Venezuela, and Brazil, reviewed by Rohwer (1988), who accepts *Systemonodaphne* as the valid name for this genus. The cupule is cupshaped, with a double margin and persistent, reflexed tepals. Arguments for rejecting the name *Systemonodaphne* are discussed by van der Werff (1986).

Licaria Aublet

A neotropical genus of about 40 species, revised by Kurz (1983). It occurs from southern Florida and Mexico to southern Brazil and Bolivia. The cupule is cupshaped and has a double margin; however, in some species the double margin is scarcely noticeable. A few species have opposite leaves.

Lindera Thunberg

Lindera is represented by three species in eastern North America and an additional hundred in Asia. The fruit is seated on a small, platelike cupule. Two of the American species are rare; one was only recently described (Wofford, 1983). Twigs, leaves, and fruits of the common American species are used to prepare a fragrant tea.

Litsea Lamarck

In the New World *Litsea* is represented by about five species, known from the U.S.A., the mountains of Mexico, and Costa Rica. Most species (several hundred) occur in Asia south to Australia and the Pacific Islands. The fruit is subtended by a cupshaped cupule. Leaves of *Litsea glaucescens* are used as a spice, similar to bay leaves.

Mezilaurus Taubert

A neotropical genus of 16 species occurring in the Amazon basin (including Bolivia, Peru, Colombia, Venezuela, and the three Guyanas), revised by van der Werff (1987a). The fruit is seated on a small, platelike cupule. The flowers are very similar to those of *Licaria*, but the two genera differ in cupule shape, leaf position, inflorescence type and wood anatomy. All species have leaves clustered at tips of branches. Two species with 4-celled anthers were recently transferred to *Williamodendron* (Kubitzki & Richter, 1987).

Nectandra Rol. ex Rottb.

A large, neotropical genus of about 120 species, currently under revision by J. Rohwer. It occurs from southern Florida and Mexico to Argentina. Fruits are seated in a cupshaped (sometimes small) cupule. Tepals are spreading at anthesis.

Ocotea Aublet

The largest genus of Lauraceae in the Neotropics, with at least 300 species. It is also known from Madagascar and tropical Africa. The genus is very variable and serves as a dumping ground for species that cannot be readily accommodated in other genera. Its distribution in the Neotropics is from Mexico and southern Florida to Argentina. Shape and size of cupule is variable and ranges from small and platelike to cupshaped, sometimes with a double margin or with persistent tepals. Tepals are erect or spreading at anthesis.

"*Paraia*"

A monotypic genus known from Amazonian Brazil. The cupule has a double margin with persistent tepals. Tepals are erect at anthesis.

Persea Miller

An incompletely understood genus with at least 80 neotropical species, but better represented in Asia and with one species in the Canary Islands. The fruit can be seated on a naked pedicel (as in *Persea americana*, the type species) or is subtended by persistent, indurate tepals (as in the great majority of species). A cupule is never present. A worldwide survey is needed to determine if *Machilus* belongs in *Persea* (as is accepted here) or should be recognized as a distinct genus. The neotropical species have been revised by Kopp (1966). *Persea*

americana is widely cultivated for its edible fruit. A few neotropical species have clustered leaves.

Phoebe Nees

Phoebe is here considered a palaeotropical genus. Neotropical species formerly placed in *Phoebe* are, for the larger part, included in *Cinnamomum*; a few belong to *Ocotea*.

Phyllostemonodaphne Kostermans

An infrequently collected, monotypic genus from the Atlantic rainforests in southern Brazil. The fruit is seated in a double-rimmed cupule. The genus was revised by Rohwer (1988).

Pleurothyrium Nees

A neotropical genus with close to 40 species, known from Guatemala south to Peru, Bolivia, and Brazil. The fruit is seated in a rather deep, cup-shaped cupule, which is often warty or lenticellate. Several species have a pronounced marginal vein, an unusual feature in Lauraceae, or clustered leaves. The genus is being revised by van der Werff.

Povedadaphne Burger

A monotypic genus apparently restricted to Costa Rica. The rather large fruit is subtended by a small, platelike cupule. The fruiting pedicel is swollen. Distinctive are the nine columnar stamens, each with four apical locelli.

Rhodostemonodaphne Rohwer & Kubitzki

A poorly known genus of about a dozen species, two of which are rather common, while several species are in need of description. The genus has been reported from Costa Rica to Brazil and Peru. The cupule is deeply cupshaped and rather large.

Sassafras Presl

A small genus with three species, one widespread in the eastern U.S.A., the other two in China. Leaves are frequently lobed. The cupule is cup-shaped, often crowned with remnants of the tepals. Bark and root have been used to prepare tea or root beer.

Systemonodaphne

See *Kubitzkia*.

Umbellularia Nuttall

A monotypic genus occurring in California and southern Oregon (U.S.A.). The fruit is subtended by a small, platelike cupule. The leaves are used as a spice; the wood is valued for cabinetmaking.

Urbanodendron Mez

A neotropical genus of three species, restricted to southern Brazil. The cupules are known in two species: double-rimmed, with more or less persistent tepals. The genus has been revised by Rohwer (1988).

Williamodendron Kubitzki & Richter

A neotropical genus with two species, infrequently collected, but known from Costa Rica, northern Colombia, Amazonia, and southern Brazil. The number of species will likely increase as more collections become available. The cupule is small and platelike, resembling that of *Mezilaurus*. Leaves are clustered at the tips of branches.

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TWO NEW GENERA OF NEOTROPICAL LAURACEAE AND CRITICAL REMARKS ON THE GENERIC DELIMITATION[1]

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ABSTRACT

Two genera, *Chlorocardium* and *Paraia*, are described, illustrated, and discussed. *Chlorocardium* includes two species previously placed in *Ocotea* and is known from Guyana and Surinam (*C. rodiei*), and Ecuador (*C. venenosum*). *Paraia* includes one species, *P. bracteata*, from the States of Pará and Amazonas, Brazil. Problems with generic placement of several other species are discussed. The usefulness of two-celled vs. four-celled stamens as a character to define genera is discussed, and examples of polyphyletic genera based solely on the two-celled condition are given.

The genera of the Lauraceae, with very few exceptions, are circumscribed by a combination of characters rather than by single exclusive characters. However, Kostermans (1957) noted that "Apparently the combination of characters is more or less indefinite, and almost all combinations are represented." Although this statement must not be taken literally, because in strictly mathematical terms millions of combinations would be possible with the given characters, it does emphasize the reticulate variation within the family. Naturally, not all combinations are equally frequent. The more frequent combinations correspond to the larger genera, while rare combinations have been treated in two different ways. They either have been placed in a genus of their own (e.g., *Anaueria*, *Dicypellium*, *Phyllostemonodaphne*, *Urbanodendron*), or they have been included as aberrant species in one of the larger genera. In the present paper we describe two new genera based on rare combinations of characters, and we discuss some of the discordant elements in larger genera, as well as several cases of unsatisfactory generic delimitation.

The first of our new genera has the most unusual flower structure. Ironically, it is based on a species that normally would be considered to be among the better known Lauraceae.

Chlorocardium Rohwer, Richter & van der Werff, gen. nov. HOLOTYPE: *Chlorocardium rodiei* (Schomb.) Rohwer, Richter & van der Werff.

Ceteris Lauracearum generibus differt foliis oppositis, floribus exinvolucratis tetrameris vel plerumque irregularibus, staminibus 12–20, verticillis 3–5 dispositis, subaequalibus, omnibus quadrilocellatis latrorso-extrorsis, sessilibus, basi biglandulosis, ovario pubescente.

Chlorocardium rodiei (Schomb.) Rohwer, Richter & van der Werff, comb. nov. BASIONYM: *Nectandra rodiei* Schomb. in Hook., London J. Bot. 3: 616. 1844. TYPE: Guyana. 20–50 mi. inland, along the rivers Essequibo, Cuyuni, Demerara, Pomeroon, Berbice, *Schomburgk 1004* (holotype, K; isotypes, G, L; probable isotypes with no. *1703* in B, GZU).

Nectandra leucantha var. *rodiaei* (Schomb.) Griseb., Fl. Brit. W. I. 282. 1860.

Ocotea rodiei (Schomb.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 236. 1889.

Chlorocardium rodiei is a species of considerable economic importance. Its wood ("Greenheart," hence the name *Chlorocardium*) is among

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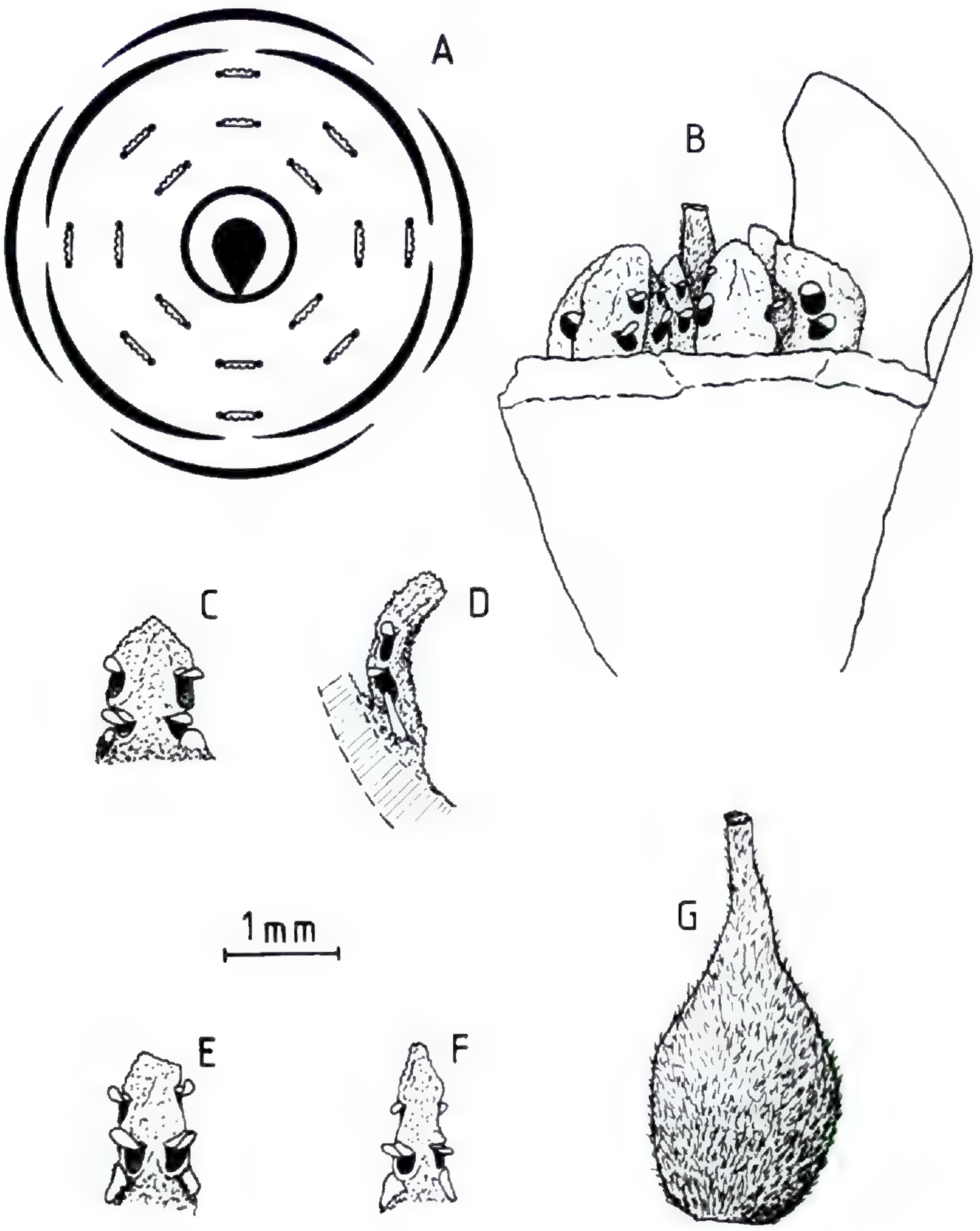

FIGURE 1. *Chlorocardium rodiei*.—A. Floral diagram of a regular flower with four whorls of stamens with four stamens each.—B. Flower, nearly all tepals removed.—C. Stamen of the first whorl, seen from outside.—D. Stamen of the first whorl, seen from side (note placement on the inside of the floral tube).—E. Stamen of the third whorl, seen from outside.—F. Stamen of the fourth whorl, seen from outside.—G. Ovary. Voucher: *Pipoly 7530*.

the most important commercial timbers in the family. Although the species has been known for more than 200 years, it is still poorly represented in the major herbaria, and very few flowering collections are known. This scarcity of flowers permitted a misinterpretation perpetuated until today. Schomburgk mentioned in the original description that most flowers appeared to be abnormal, with more than the usual number of parts. Similar statements can be found in all subsequent accounts on the species. Until today everyone who dissected a flower (including one of the authors) believed that he or she had picked a monstrosity when the flower turned out to be tetramerous or irregular, yet no one wanted to dissect a second flower because there was so little material.

As it turns out now, with more material available, the only regular flowers are indeed tetramerous (Fig. 1A), and irregular flowers are common in all specimens. Bentley & Trimen (1880) described the flower as trimerous, with nine fertile stamens. We could not find this condition. Of the 14 flowers that we examined only one appeared to be trimerous, but it had 12 fertile stamens. Eight flowers were clearly tetramerous, of these we found:

1 with 4 tepals and 4 whorls of 4 stamens each
2 with 8 tepals and 3 whorls of 4 stamens each
3 with 8 tepals and 4 whorls of 4 stamens each
2 with 8 tepals and 5 whorls of 4 stamens each.

The remaining five flowers were irregular, usually with less than the full number of stamens in the inner whorls. One of the irregular flowers had only six tepals, and another had eight tepals but four whorls of five stamens each. Tepals with one or two apparently fully developed pollen sacs were found in both a regular and an irregular flower. The stamens (Fig. 1C–F) are almost equal, broadly sessile, and more or less tongue-shaped, each with two rather inconspicuous glands at the base and

with four locules, of which the upper ones are latrorse and the lower ones latrorse-extrorse. Toward the center of the flower the stamens become slightly smaller, and the inner whorls are inserted at successively lower levels within the floral tube. This configuration is reminiscent of the closely related Monimiaceae, but without parallel in the Lauraceae. It may be interesting to note that also the native name in Guyana is shared with a Monimiaceae. It is reported to be "Bebearu," "Bibiru," "Sipeira," "Sipiri," or "Sipiru"—undoubtedly the same root from which Aublet (1775) derived the name *Siparuna*.

Schomburgk reported that in times of food shortage the seeds of the Greenheart tree were used by the natives in a way similar to cassava, i.e., they were grated, and the starch was repeatedly washed to deprive it of the bitter alkaloids.

There is some uncertainty concerning the spelling of the specific epithet. The species is named for "Dr." Rodie, a Royal Navy physician who first described the medicinal uses of the plant. In the original publication the epithet is spelled "*rodioei*," with the oe printed as one character. Sandwith (1939) suggested that this was indistinguishable from ae, and that the correct spelling should be "*rodiaei*," because the name Rodie would be latinized as "Rodiaeus." However, from the following text of the description it is obvious that oe and ae are indeed different characters. Since the spelling with oe lacks any foundation, we suggest that [in accordance with Art. 73.10. of the *Code* (Greuter, 1988)] it should be corrected to "*rodiei*," as has been done by Mez (1889) and most subsequent authors.

The second species of the genus *Chlorocardium* is poorly known:

Chlorocardium venenosum (Kosterm. & Pinkley) Rohwer, Richter & van der Werff, comb. nov. BASIONYM: *Ocotea venenosa* Kosterm. & Pinkley, Bot. Mus. Leafl. Harvard Univ. 22: 241. 1969. TYPE: Colombia. Putumayo: Río Guamúes, Santa Rosa, alt. 1,060 ft., 77°05′W, 00°19′N, 26 Nov. 1966, *Pinkley 555* (holotype, GH; isotypes, ECON, S, U).

In the original description of this species the authors state that "Most of the flower buds available for dissection were abnormal as a result of fungal attack." In fact, they are so few and immature on the type specimen that it does not look worthwhile to dissect any of them. The general aspect of the plant agrees very well with *Chlorocardium rodiei*, and the wood structure described leaves no doubt that the two species are extremely close. *Chlorocardium venenosum* is known only from the border region of Colombia and Ecuador, while we have seen material of *Chlorocardium rodiei* only from Guyana. It also occurs in Surinam, but reports of a much wider distribution (as in Mell & Brush, 1913) appear to have no foundation.

The structure of the secondary xylem of the two species described here under *Chlorocardium* is highly unusual in two aspects: The interconnecting pit pairs between vessels as well as between vessels and parenchyma cells (rays and axial parenchyma) are extremely small (3–4 μm diam.), a condition absent not only from *Nectandra* and *Ocotea*, but from all Lauraceae with the exception of the small Asiatic genus of *Neocinnamomum*. More importantly, parenchyma cells are connected to adjacent vessels through unilaterally compound pitting with large, simple pits subtending two or more of the small bordered pits in the vessel elements. These large pits in the parenchyma cells are often traversed by branched or simple filiform protrusions of cell wall material. In addition, vessel elements in both species bear at the ends a partial or complete ring of large, windowlike pits that give the impression of a crown or corona, hence the term "coronated vessel elements" used by Kostermans et al. (1969) to describe this phenomenon quite unique in xylem anatomy.

The other aspect considered here is the complete lack of secretory cells in the secondary xylem. What might have been a chance observation for *Chlorocardium venenosum* described from only one specimen so far (Kostermans et al., 1969) becomes significant for *C. rodiei*: The countless descriptions dealing with the secondary xylem of this taxon have not once revealed the presence of secretory cells. Thus their absence, although generally not diagnostic in Lauraceae, might justly be used in conjunction with other characters to seriously question the traditional taxonomic affinities of these two species.

These findings are corroborated by the equally unusual structure of the secondary phloem of *C. rodiei* (for detailed description see Richter, 1981), which is characterized by special features different from the prevailing structural patterns in Lauraceae, among them the complete lack of secretory cells (sic).

Thus, the wood and bark structure supports a rather isolated position for *Chlorocardium*, but unlike the flower structure it does not suggest an affinity with the Monimiaceae.

Fruits of *Chlorocardium rodiei* have been described as large (6–7 cm long, 5 cm diam.) and

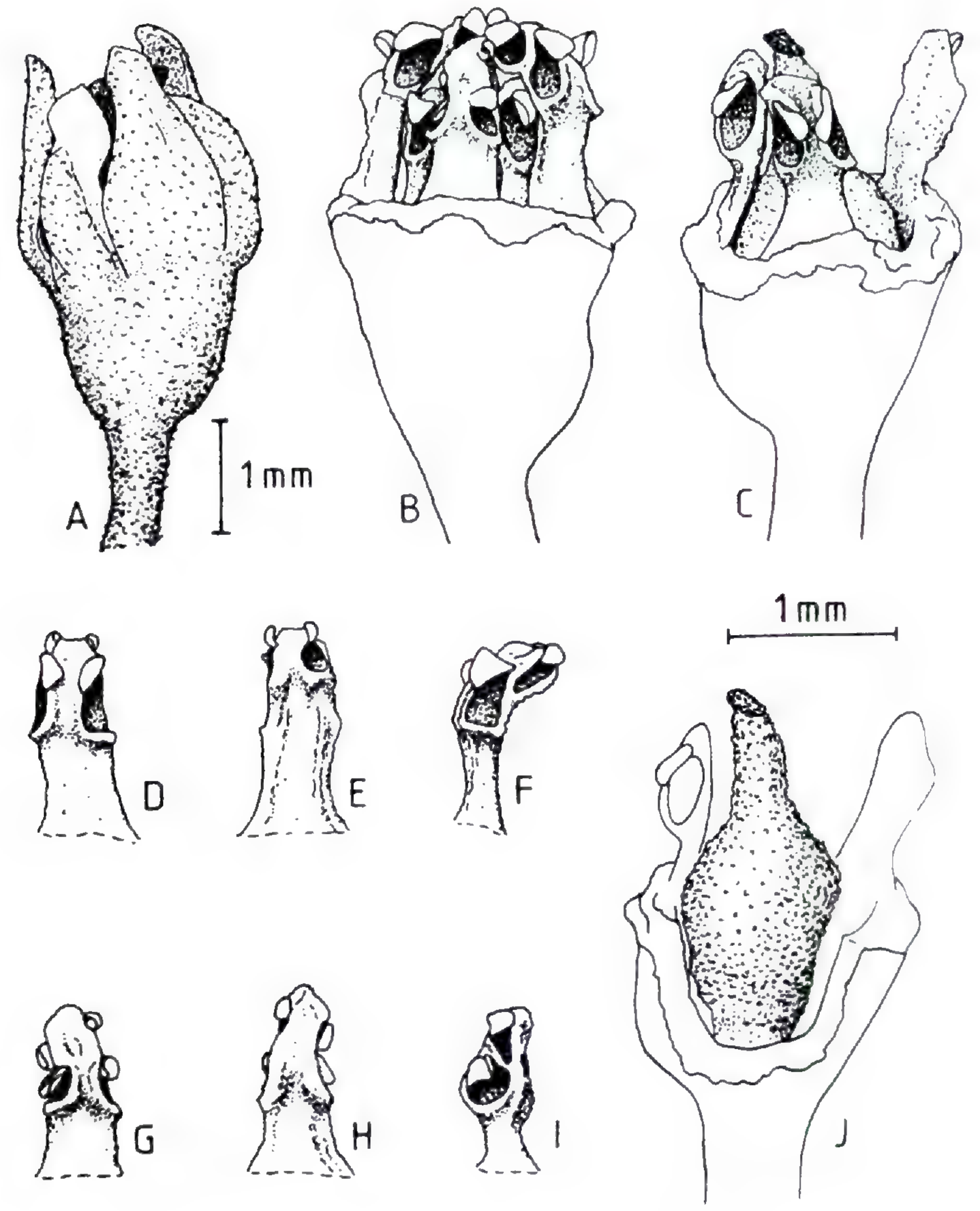

FIGURE 2. Undescribed new genus.—A. Flower.—B. Flower, tepals removed.—C. Receptacle with ovary, outer stamens removed.—D. Stamen of the first whorl, seen from outside.—E. Stamen of the first whorl, seen from inside.—F. Stamen of the first whorl, seen from side (curved inward).—G. Stamen of the second whorl, seen from outside.—H. Stamen of the second whorl, seen from inside.—I. Stamen of the second whorl, seen from side.—J. Ovary, its position in the receptacle schematically shown. Voucher: *Vásquez 6020*.

ellipsoid to ovoid-globose, seated in a shallow, single-margined cupule, 2–2.5 cm diam. (Mez, 1889; Kostermans, 1936). A recently collected specimen (*Pipoly 8616*, MO) shows a not very deep, lenticellate cupule, ca. 1.5 cm diam. and a clearly exserted, ovoid fruit, ca. 1.5 cm long. Fruits and cupule are attached to the twigs. The tree was still flowering at the time of collection, and it is possible that the fruits were immature. Fruits of *C. venenosum* were described as depressed-globose, 4.5 cm high and 5.5 cm diam., almost completely enclosed by the cupule. A recent collection with fallen fruits agrees very well with this description; the fruits are up to 6 cm high and 7 cm diam., the cupule largely encloses the fruit, leaving an orifice of about 2.5 cm diam. Fruits are used by the Kofan Indians to make arrow poison. The very large cupule of *C. venenosum* readily separates this species from *C. rodiei* with its much smaller, shallow cupule. With the exception of the recently described *Ocotea megacarpa*, fruit size of the two *Chlorocardium* species far exceeds that of any *Ocotea* or *Nectandra* species.

Recently we found another species with opposite leaves and variable staminal configuration that in some characters resembles *Chlorocardium* but also shows marked differences (Fig. 2). Like in all other neotropical Lauraceae (except *Chlorocardium*) the flowers are trimerous, invariably with six tepals and not more than three whorls of fertile stamens. The fourth whorl, which in many Lauraceae is staminodial, seemed to be represented only in the fragments of one broken flower. In 25 reasonably intact flowers examined we found the following configurations:

10 flowers with whorl I and II 4-locular, whorl III 2-locular

8 flowers with whorl I and II 4-locular, whorl III absent
4 flowers with all three whorls 4-locular
2 flowers irregular

In the 2-locular stamens it is the upper pair of locules that is lost. The lower pair, like in *Chlorocardium*, is latrorse-extrorse in all stamens; the upper pair can be latrorse or latrorse-introrse. Like in *Pleurothyrium* the flaps open toward the abaxial side of the stamens. The outer stamens (especially whorl I, Fig. 2D–F) are bent inward, overarching the inner stamens. All stamens have distinct, broad filaments, and there is no trace of glands. The large ovary is inserted in a deep, cup-shaped receptacle. All parts of the flower, including the ovary and the inside of the receptacle, are covered with papillae.

This combination of characters is unique within the family, and we have no doubt that our material represents a new genus. However, as our observations are based on only one collection (*R. Vásquez 6020*), we postpone the formal description until more material becomes available.

The second new genus that we describe in this paper is far less unusual in its staminal configuration. Yet its combination of characters does not fit any of the known genera.

Paraia Rohwer, Richter & van der Werff, gen. nov. HOLOTYPE: *Paraia bracteata* Rohwer, Richter & van der Werff.

Ceteris Lauracearum generibus differt foliis in apice ramulorum subverticillatim congestis, floribus subglobosis bracteis conspicuis plerumque numerosis subtentis, tepalis margine hyalinis interne epapillosis glabrisque, staminibus novem, antheris quadrilocellatis locellis arcuatim juxtapositis, ovario bene evoluto in tubo profundo, cupula duplicimarginata margine exteriore longiore et perianthii segmentis auctis sexlobato.

Paraia bracteata Rohwer, Richter & van der Werff, sp. nov. TYPE: Brazil. Pará: Mun. Oriximiná, Rio Trombetas, right bank, Porto Trombetas, road to Mineração Rio Norte, km 60, beyond Bauxite mine, 29 Aug. 1980 (fl, fr), *Cid et al. 1890* (holotype, MO; isotypes, HBG, INPA *96058* not seen, NY). Figures 3, 4.

Frutex vel arbor ad 8 m (20 m?) alta. Ramuli teretes, hornotini gemmaeque dense ferrugineo tomentosi. Folia petiolis crassiusculis 5–13 mm longis canaliculatis, fere omnia apice ramulorum congesta, oblanceolata vel obovata vel oblonga, adulta 14–35 cm longa, 5–12.5 cm lata, apice ex acuto vel obtuso manifeste acuminata, basi cuneata vel rarius acuta (basi ipso interdum obtusa), in sicco ± olivacea, adulta supra opaca vel nitidula glabra, subtus peropaca subglabra, margine plano, nervis secundariis utroque costae latere 6–11 e nervo medio sub angulo 40–80° prodientibus. Inflorescentiae e gemmae terminali squamarum axillis prodientes, anguste thyrsoides, quam folia multo breviores (3–11 cm longae, pedunculis 1.2–8 cm longis), dense ferrugineo-tomentosae. Flores breviter pedicellati vel subsessiles in apice inflorescentiae ramulorum ± glomerati, bracteis conspicuis subtenti, plerumque tubo receptaculi conspicuo. Perianthium flore plena subglobosum, haud patens, 2–3.5 mm diametro. Tepala suborbiculares, basi crassa, margine hyalino, externe basi et linea media tomento ferrugineo, interne epapillosa glabraque. Stamina novem, ca. 0.8–1.5 mm longa, epapillosa, quadrilocellata vel serie prima raro bilocellata, sex exteriora eglandulosa filamentis gracilibus locellis subapicalibus arcuatim vel linea unica juxtapositis, tria interiora basi biglandulosa filamentis crassiusculis locellis subapicalilateralibus. Staminodia parva, subulata, dense tomentosa. Receptaculi tubus profundus, saltem longitudine staminum, angustus, intus dense tomentosus. Pistillum glabrum, elongatum, ca. 2–2.4 mm longum, stylo ovarium aequante vel eo paulo longiore. Cupula obconica vel subhemisphaerica, 12–15 mm diametro, 6–8 mm profunda, duplicimarginata, margine exteriore longiore et perianthii lobis incrassatis manifeste sexlobato. Bacca ellipsoidea vel plerumque ovoidea, ca. 14–24 mm longa et 10–12 mm diametro.

Shrub or small tree, usually to ca. 8 m tall (only *Silva 2220* from a tree 20 m tall). Twigs round, the youngest with a dense cover of long (ca. 0.4–1 mm long), straight to curled, ± erect, relatively thick, reddish brown hairs, quickly becoming felt-like, easily worn off. Terminal buds covered by relatively large (4–7 mm) scales, somewhat spreading, with the same kind of indument as the twigs on outside (though not always dense at the margins), glabrous on inside. Leaves drying with a characteristic grayish green to olive-brown color, alternate but with few exceptions clustered at the tip of the branchlets (sometimes a second, older whorl still present), 14–35 cm long, 5–12.5 cm wide, ca. 2.3–4(–4.5) times longer than wide, oblanceolate, obovate or oblong, widest in the middle or mostly slightly above, toward the apex acute to obtuse, the tip itself with a distinct acumen, base mostly long, ± cuneate or sometimes acute (at the very base occasionally abruptly obtuse), lateral veins 6–11 on each side of the midrib, diverging at 40–80°, midrib and secondaries above ± slightly impressed but the vein itself convex, below prominent, tertiary reticulation above almost invisible to impressed and slightly convex, below slightly raised to prominent. Indument of leaves consisting of the same kind of hairs as on the twigs, even in the youngest leaves above sparse, sometimes dense on midrib, below moderately sparse and highly unevenly distributed, often dense on midrib, or sometimes subglabrous from the beginning; mature leaves entirely glabrous or below often with rudiments of the indument. Inflorescences springing from the

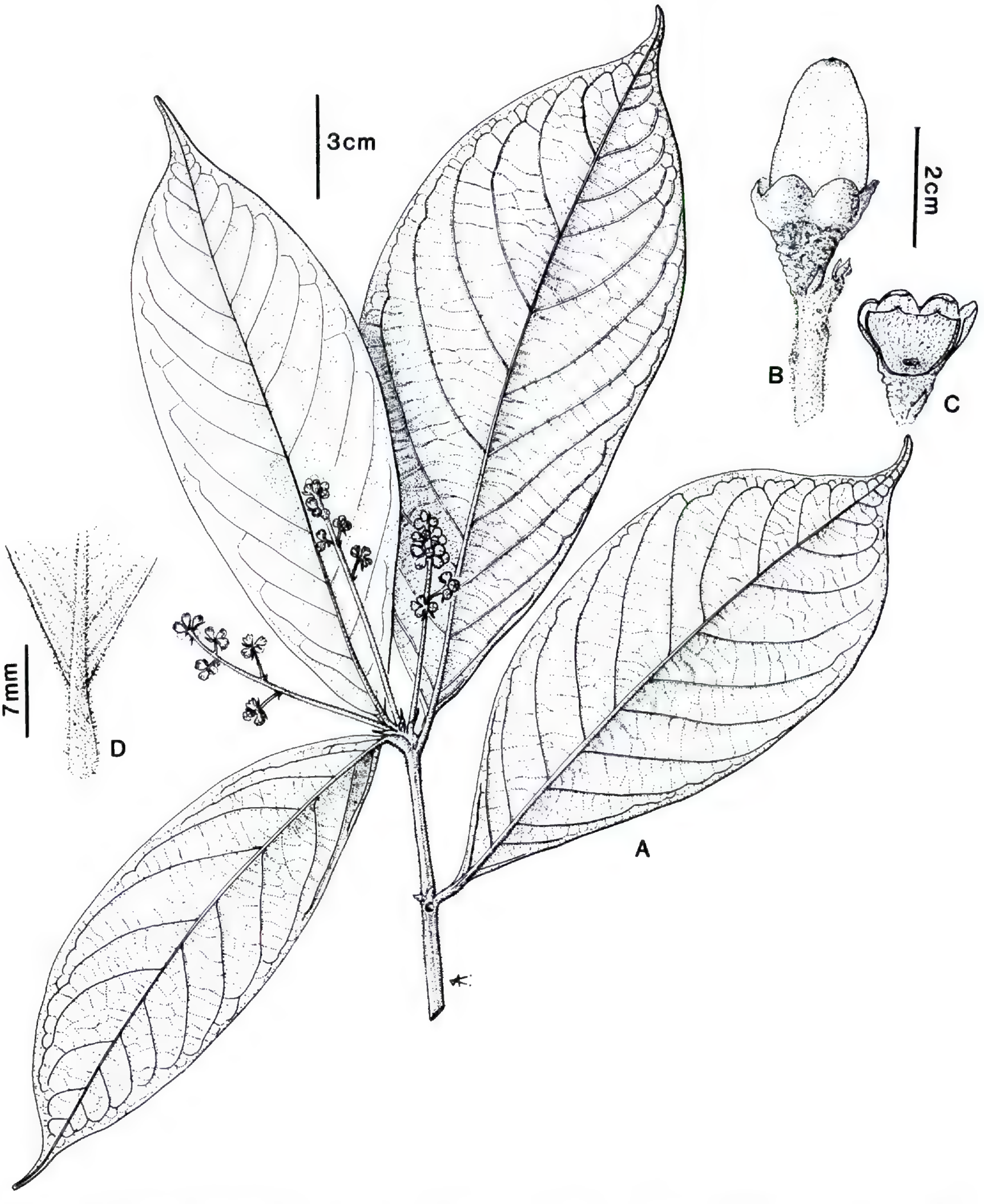

FIGURE 3. *Paraia bracteata*.—A. Habit.—B. Fruit.—C. Cupule, cut open, showing the double margin.—D. Detail of leaf base. Vouchers: A, D, *Cid 1890*; B, C, *A. S. Silva et al. 72*.

scales of the terminal bud, 2–8(–11) cm long with a peduncle of 1.5–5.5(–8) cm, narrowly thyrsoid, the lateral branches not more than 1 cm long (at anthesis; often enlarged afterward). Flowers apparently bisexual (but see below), sessile or with a short pedicel (to 1 mm), clustered at the tip of the inflorescence branches, subtended by relatively large bracts, which are often more numerous than the flowers but (at least partly) fall off during anthesis. Perianth subglobose, ca. 2–3.5 mm diam., opening only slightly during anthesis. Tepals 6, suborbicular, fleshy at the base, hyalinous toward the margins, only on the outside at the base and in the middle with reddish hairs, otherwise glabrous, with-

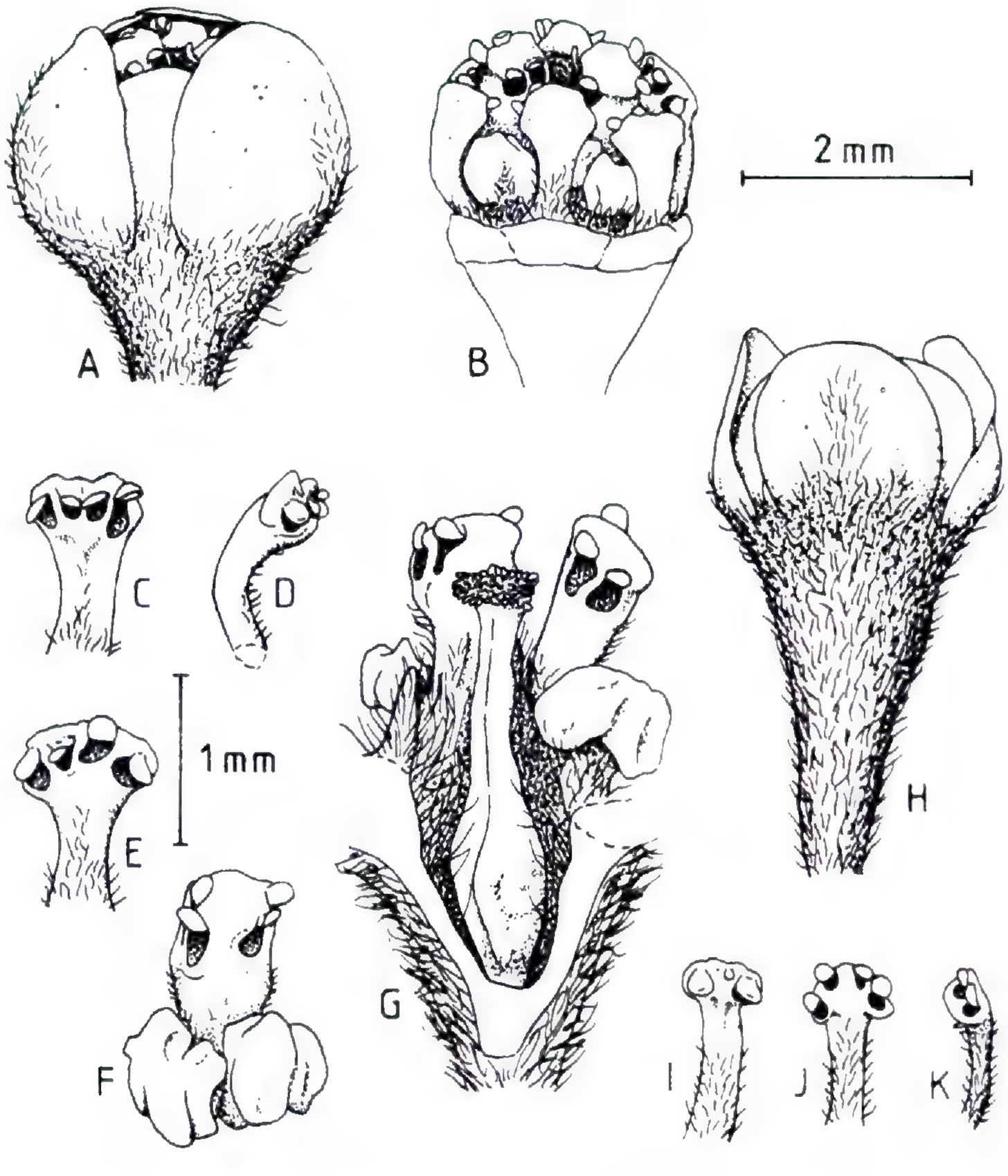

FIGURE 4. *Paraia bracteata*.—A. Flower, globular form.—B. Flower, tepals removed.—C. Stamen of the first whorl (of A), seen from inside.—D. Stamen of the first whorl, seen from side.—E. Stamen of the second whorl, seen from inside.—F. Stamen of the third whorl, seen from outside.—G. Receptacle with ovary, staminode and two inner stamens, cut open, tepals and outer stamens removed.—H. Flower, elongate form.—I. Stamen of the first whorl (of H), 2-locular form, with a rudimentary third locule, seen from inside.—J. Stamen of the second whorl, seen from inside.—K. Stamen of the second whorl, seen from side. Vouchers: A–G, *Cid 1890*; H–K, *Ducke s.n.*

out any papillae. Stamens 9, 4-thecous or in the first whorl rarely 2-thecous, without papillae, the outer six 0.8–1.4 mm long, their slender filaments 0.5–0.8 mm long, at least at the base and on adaxial side with some hairs, the anthers wider than long, thecae subapical, introrse, arranged in an arc or (especially in the first whorl) almost in a horizontal line, the inner three stamens 0.8–1.6 mm long, their filaments thick, only slightly narrower than the anther, 0.4–0.8 mm long, at least laterally hairy, each with a pair of conspicuous glands at its base, the thecae subapical in two ± lateral pairs, almost at the same level (the adaxial ones slightly higher than the abaxial ones). Staminodia three, 0.3–0.6 mm long, subulate, very hairy. Receptacular tube 1.2–2 mm deep, narrow, densely hairy inside. Pistil slender, ca. 2–3.4 mm long, style as long as the ovary or slightly longer. Cupule broadly obconical to subhemispherical, 12–15 mm diam., 6 –8 mm deep, distinctly double-rimmed, the outer margin longer, crowned by enlarged tepals (which, however, seem to break off easily). Berry ellipsoid to ovoid, 14–24 mm long, 10–12 mm diam., often with truncate tip.

Additional specimens examined. BRAZIL. AMAZONAS: Manaus–Itacoatiara Highway, Colonia Santo Antonio, 27 Oct. 1966 (fr), *Allen & L. Coêlho 330* (HBG, NY); Rio Cuieiras–Manaus trail, km 1, 6 Apr. 1974 (fl), *Campbell et al.* in *Prance 21901* (HBG, MO, NY); Manaus, Estrada de Flores (Rosa de Maio), Feb. 1974 (st), *D. Coêlho s.n.* (HBG, INPA *46534*), near Igarapé Mindú, 12 July 1929 (fl), *Ducke s.n.* (U), along road to Aleixo, 12 Aug.–1 Sep. 1936 (fr), *Krukoff 7996* (F, NY); Rio Cuieiras, 2 km below mouth of Rio Brancinho, 11 Sep. 1973 (fl), *Prance et al. 17749* (HBG, NY); Manaus, Igarapé do Bindá, 19 Oct. 1961 (fr), *Rodrigues & Chagas 2666* ≡ *3466* (HBG, INPA *10016*, NY); Manaus–Caracaraí road, km 19, 20 Sep. 1961 (fr), *Rodrigues & L. Coêlho 3317* (NY). PARÁ: Belém, Instituto Agronômico do Norte, 3 Aug. 1962 (fl juv.), *Allen 79* (NY); Mun. Oriximiná, Rio Trombetas, left bank, at Lago Moura, 22 Aug. 1980 (fl), *Cid et al. 1825* (HGB, MO); Lago Cuçarí, Planalto de Santarém, area of forest inventory by IAN, SPVEA, and FAO, 15 Apr. 1955 (fl), *Fróes 31668* (NY); Mocambo, EMBRAPA Forest Reserve, ca. 10 km from Belém, 13

Nov. 1984 (st), *Gentry 48956* (MO), 10 Oct. 1966 (fr), *Pires & N. T. Silva 10245* (HBG), 28 Sep. 1967 (fr imm.), *Pires & N. T. Silva 10947* (NY), 2 Sep. 1967 (fr), *Pires & N. T. Silva 10949* (NY), 3 Aug. 1973 (fl), *Pires 13219* (HBG, NY); Mun. Almerim, Estrada do Pedrão, km 40, 12 Nov. 1978 (fr), *Santos 284* (F); Serra dos Carajás, 13 km from AMZA headquarters, road to sawmill, 18 Oct. 1977 (fr), *A. S. Silva et al. 72* (HBG, MO); Santarém, Estrada do Palhão, km 35, near Igarapé Curupira camp, 24 Aug. 1969 (fr), *M. Silva & Souza 2402* (HBG, MO, NY); Rio Jarí, Monte Dourado, Planalto B., between Pilão and Repartimento, 28 Oct. 1968 (fr), *N. T. Silva 1328* (HBG, NY); Jarí, road from Bandeira to Pilão, km 39, 18 June 1969 (fl, fr imm.), *N. T. Silva 2220* (HBG, NY).

WOOD DESCRIPTION

The wood and bark descriptions are based on the type collection only. The specimen comes from a small tree ca. 7 m tall. The wood sample has an average diameter of 7 cm, covered by a grayish brown bark ca. 3 mm thick. Wood and bark are slightly aromatic.

General. Wood uniformly yellowish brown; heartwood probably dark brown as indicated by the presence of darker colored patches around a zone damaged by insect larvae; evenly textured, dense and heavy (specific gravity ca. 0.85/cm^3).

Anatomy. Wood diffuse porous throughout, pores evenly distributed, thin-walled and angular in outline; solitary and radial multiples of 2–5 in variable proportions; largest pores 100–150 μm diam., frequency 15–22/mm^2. Vessel perforations exclusively simple; intervascular pits invariably alternate, mostly circular in outline and not crowded, pit apertures included; pits 9–11 μm diam. Tyloses common, thin-walled to sporadically sclerotic; no gum deposits observed. Fibers libriform, of medium wall thickness; regularly septate; generally ca. 15 μm diam., rarely up to 20 μm; pits very small and inconspicuous, mostly confined to radial walls; growth increments distinct microscopically, marked by 1–2-seriate tangential bands of wide-bodied fibers (up to 30 μm diam.); no imperforate tracheary elements observed. Parenchyma basically paratracheal sparse to irregularly vasicentric; rather inconspicuous unless interspersed with large idioblasts (oil cells) as part of the vasicentric sheath; vertical strands composed of 4–6 individual cells; pits to vessels enlarged, oval to gashlike and extended horizontally. Wood rays predominantly biseriate, heterogeneous with 1–2, rarely up to 4, marginal rows of upright and/or square cells; height of largest rays 0.5–0.8 mm; vessel ray pits enlarged, oval to irregular or gashlike; reddish brown gum deposits sometimes present. Crystalline deposits and silica absent. Oil cells common, associated with axial and ray parenchyma; very large with diameters up to 70 μm and axial extensions up to 0.35 mm (associated with marginal ray cells) and 0.70 mm (associated with parenchyma strands).

BARK DESCRIPTION

Secondary phloem ground tissue composed of conducting (sieve and companion) cells and phloem parenchyma. Interspersed are numerous oval or diamond-shaped, rarely tangentially extended sclereid islands consisting of vertically elongate, columnar sclereids. Secondary phloem fibers are absent. Toward the periphery the secondary phloem is delimited by a continuous ring of small, irregularly shaped and largely isodiametric sclereids enclosing few and widely spaced groups of primary phloem fibers. The sclereid ring is followed by cortical parenchyma gradually phasing into several rows of rectangular, radially oriented phelloderm cells (replete with dark colored gum deposits or sclerified) and a narrow (2–3 rows of similar but empty cells) terminal phellem. Just inside the sclereid ring few isolated radially flattened sclereids are present. Phloem rays resemble wood rays in dimensions and composition. Their radial course through the secondary phloem is ragged due to the spatial rearrangement of other constituents following the early collapse of conducting tissues. Ray cells become sclerified when traversing sclereid islands. Oil cells are scattered throughout the secondary phloem and the cortical parenchyma. Crystalline inclusions are deposited in ray and axial parenchyma in considerable quantities, usually as minute acicular crystals.

Note. The sclereid island constituents (columnar sclereids) are more or less rectangular in cross section, with the larger side extending in radial direction. The narrow tangential faces have pointed ends, thus resembling fibers in tangential view. The polylamellate structure of the cell wall, the distinct pit canals, and the type of lignification exposed by differential staining, however, betray their probably parenchyma-derived sclerenchymatic nature.

Paraia bracteata was first recognized as a new species by Beulah Coe-Teixeira. She annotated several specimens as *Nectandra paraensis* Coe-Teixeira, but she never published the name. While working toward a revision of the genus *Nectandra*, J. Rohwer found that this taxon has nothing in common with *Nectandra* except the technical character of "four locules of the anther arranged in an arc." There are no other species of *Nectandra* with the leaves distinctly crowded at the tip

of the branchlets, with hyalinous tepals entirely lacking papillae, or with clearly double-rimmed cupules. Also, the general aspect of the plant, its flowers or flower parts, do not suggest *Nectandra*. Sterile material is often annotated as *Aniba*, which can be quite similar. Vegetatively and even in its inflorescences *Paraia bracteata* strikingly resembles *Rhodostemonodaphne miranda* (Sandw.) Rohwer, but this similarity does not extend to the inner organization of the flower. After discussing the possible relationships of this new species, we concluded that we would have to describe it as a new genus. For every known genus we could find at least three important reasons why it should not be included there.

Judged by its rather commonplace lauraceous wood structure alone, *Paraia bracteata* cannot be safely differentiated from all but a few neotropical Lauraceae, e.g., *Mezilaurus*, *Clinostemon*, *Caryodaphnopsis*. Nearly all positive and negative affirmative characters circumscribing the prevailing structural patterns of Lauraceae are present. In combination with the very specific bark structure, however, most neotropical genera of this family can be excluded as possible matches. Very good structural agreement can be found only in a small group of taxa comprising most species of *Aniba* and *Licaria*, and a few species currently ascribed to *Ocotea*. When taking into account the less diagnostic but nevertheless helpful general wood characters such as color and density, the scope can be narrowed down further to the few species constituting subg. *Canella* of *Licaria* (Kurz, 1982; Richter, 1985), and two strikingly similar species of *Aniba* (*A. canelilla* (HBK) Mez, *A. ferrea* Kubitzki). Even without supporting evidence from exomorphic characters, an attribution to the genus *Nectandra*, as initially proposed by Coe-Teixeira, can definitely be ruled out.

Following the traditional "number's game" of generic delimitation, it would seem that *Paraia* was not at all close to *Licaria*, which has only three fertile stamens (whorl III), each with two thecae. Only the double-rimmed cupule would fit that genus better than any other. However, when considering additional floral characters (which have received little attention up to now), a connection between *Paraia* and *Licaria* does not seem that far off. In *Licaria* it is quite common that the tepals are short and scarcely spreading at anthesis, and that only the style protrudes beyond the nearly globular perianth. Also the thickish, columnar stamens of the third whorl with their subapical thecae are somewhat similar to *Licaria*. The fact that the stamens of the first whorl are sometimes only 2-thecous in *Paraia* indicates a tendency toward reduction. If the thecae were entirely reduced in the outer whorls, the resulting staminodia would be quite similar to those of several *Licara* species, with a slender filament and a flat, widened apex. Thus, the possibility that *Paraia* represents a more primitive offshoot of the line leading to *Licaria* cannot be ruled out.

When looked at individually, the flowers of *Paraia bracteata* appear to be invariably bisexual. However, when flowers from several different specimens are dissected, it seems that there are two types of flowers, differing in proportions. In the first type (Fig. 4A–G), the flowers are nearly globular, the receptacular tube not being apparent from the outside. The length of the stamens is approximately equivalent to the depth of the receptacle. In the second type (Fig. 4H–L) the stamens, although apparently fertile, are noticeably smaller. The receptacular tube is deeper, almost twice as long as the stamens, visible also from the outside. The ovary, however, is more or less the same size in both types. It is possible that the different proportions indicate an incipient separation of the sexes. It may, on the other hand, be just an expression of geographic differentiation. Such a differentiation is obvious in leaf shape: specimens from the surroundings of Manaus have relatively much narrower leaves than those from the state of Pará.

Discussion of Generic Delimitation in the Lauraceae

Ocotea rubra

A highly unusual combination of characters is also found in a species known as *Ocotea rubra* Mez. This species has more or less obovate, glabrous leaves, crowded at the tip of the branches. It therefore resembles *Mezilaurus* rather than *Ocotea* in its vegetative characters. The flowers, however, are unlike any other known species of Lauraceae. The tepals are shorter than the floral tube and usually more or less unequal, the outer ones smaller than the inner ones. The stamens are tongue-shaped and extremely papillose. Their four thecae are introrse and arranged in an arc on the stamens of the first and second whorl, but latrorse and in two pairs above each other in the third whorl. The staminodia of whorl four are almost as large as the inner stamens, but unlike very large staminodia in other genera they are not glandular. The ovary has a very slender style, as, e.g., in *Licaria* or *Mezilaurus*. The fruit is almost completely surrounded by a deep cupule during most

of its development, but about half exserted at maturity.

There is no other species of *Ocotea* with unequal tepals, and most of the other characters of *O. rubra* are very rare. Anatomical data (Richter, 1981) further underscore the isolated position of this species. Obviously, there is no reason to retain it in *Ocotea* other than reluctance to further increase the number of monotypic genera. In several characters (unequal tepals, broadly sessile stamens, reddish brown wood with very large cross-field and intervascular pits), *O. rubra* resembles the Asian genus *Nothaphoebe*, but the fruit is very different. *Nothaphoebe* does not have a well-developed cupule, but only a somewhat enlarged pedicel with the tepals persistent under the fruit.

TWO-LOCULAR VS. FOUR-LOCULAR ANTHERS

All of the taxa discussed above go beyond the current delimitation of the genera simply because they represent rare combinations of characters. They are therefore systematically isolated, but do not jeopardize the delimitation as such. There is, however, also an increasing number of cases that lead to serious doubts about the value of the current system. Traditionally, one of the most important characters used for the delimitation of genera is the number of thecae per anther, two vs. four. Although this character is indeed constant for the overwhelming majority of species within well-defined natural groups, its indiscriminate application may lead to artificial groupings.

Several neotropical species have the staminal configuration of one genus, yet they can be recognized as belonging to another genus based on all other characters. The current system is inconsistent in treating these species. Some are placed with their allies despite a staminal configuration that makes it impossible to key them out to the correct genus, whereas others are placed within the genus to which they would key out, regardless of their obvious affinity to species of a different genus. Thus, *Persea cuneata* Meissn., *P. bilocularis* Kopp, and *Caryodaphnopsis inaequalis* (A. C. Smith) van der Werff & Richter, e.g., have 2-thecous anthers, although their respective genera are defined by 4-thecous anthers, and *Beilschmiedia sulcata* (Ruíz & Pavón) Kosterm. is the only species with 4-thecous anthers in this otherwise 2-thecous genus.

Examples of species placed according to their staminal configuration despite obvious ties to species of a different genus are all Central American species currently placed in *Aiouea* (compare van der Werff, 1987, 1988). In nearly all of its characters, including the wood structure, *A. costaricensis* (Mez) Kosterm. is clearly a member of the *Ocotea insularis* group in the sense of Rohwer (1986). It is so close to *Ocotea skutchii* C. K. Allen as to make it very difficult to separate the two in fruit. *Aiouea lundelliana* C. K. Allen, a member of the same group, is even more obviously intermediate between the generic concepts in that its staminal configuration is variable within the same inflorescence (cf. van der Werff, 1984; Rohwer, 1986). In other Central American species of *Aiouea* the ties to a particular species or species group of *Ocotea* are not as clear, yet there is no doubt that they are closer to that genus than to the South American species of *Aiouea*.

In South America, *Aiouea* is very similar to species that used to be ascribed to the genus *Phoebe*. Again, the main difference is in the number of thecae, but it has long been known that in several of the "*Phoebe*" species only the outer anthers are 4-thecous, whereas the inner ones are 2-thecous. "*Phoebe*" is placed in quotation marks here because in the Neotropics it is anything but a good genus. The type of *Phoebe* is from Asia, and in all of the palaeotropical species the fruit is subtended by erect, enlarged, lignified tepals on a scarcely thickened pedicel, clasping the base of the fruit. Such a structure does not occur in any of the neotropical species. In some of them there are persistent tepals, but they are not enlarged, and either erect on the margin of a well-developed cupule or spreading from a swollen pedicel or a small, disklike cupule. Others have a normal, more or less bowl-shaped cupule, as in most species of *Ocotea*. Many of the neotropical species currently ascribed to *Phoebe*, in particular many Central American and Andean species, probably belong to *Cinnamomum*, as suggested by Kostermans (1961). However, transferring all of them indiscriminately to *Cinnamomum* seems rather precipitant. Some are clearly *Ocotea*, several may go to *Aiouea* after a revision of the generic delimitation, and still others may represent a genus of their own.

A third example of a probably polyphyletic genus in the New World is *Endlicheria*. It is defined by the combination of two characters, which indicate a common level of advancement rather than a common origin: (1) anthers 2-thecous, and (2) flowers unisexual. Some species of *Endlicheria* are extremely close to certain species of *Rhodostemonodaphne*. *Endlicheria metallica* Kosterm. and *R. grandis* (Mez) Rohwer can only be separated by counting the number of thecae per anther. It is questionable whether they should even be treated

as different species. Another striking similarity is found between *E. vinotincta* C. K. Allen and *R. celiana* (Allen) Rohwer. These two, although undoubtedly separate species, agree in many characters, from their reclining habit via their indument and the structure of their slender, pendent inflorescences to the development of peculiar, membranous, possibly glandular outgrowths of the filament on both sides below the anther. Especially this last-mentioned character makes it highly unlikely that the overall similarity is a mere convergence.

Other species of *Endlicheria*, e.g., *E. dysodantha* (Ruíz & Pavón) Mez and *E. pyriformis* (Nees) Mez, are much more similar to *Ocotea*, although they cannot be linked to a particular species. In *E. anomala* (Nees) Mez only the outer whorls are 2-thecous, whereas the third whorl is 4-thecous. Its fruit has a very small cupule that is lobed by the persistent bases of the tepals. Such a fruit structure is otherwise unknown in *Endlicheria*, but a rather similar form occurs in *Ocotea camphoromoea* Rohwer. This supports the view that *E. anomala* has been derived from *Ocotea* independently from other species of *Endlicheria*.

The *Endlicheria* species that form the core of subg. *Ampelodaphne* (*E. arunciflora* Mez, *E. bracteata* Mez, *E. glomerata* Mez, *E. macrophylla* (Meissn.) Mez, *E. multiflora* (Miq.) Mez, and *E. verticillata* Mez) need further investigation. With their crowded, nearly verticillate leaves and their numerous, minute flowers in profusely branched, bracteate inflorescences, they look not only unlike any other species of *Endlicheria*, but unlike any other neotropical Lauraceae at all. It is possible that they, too, have been derived from *Rhodostemonodaphne*, but independently from the species mentioned above. How the ancestral forms of this group may have looked is illustrated by *E. loretensis* O. C. Schmidt, which has been described in *Endlicheria* despite its 4-thecous anthers, based on its overall similarity to this genus.

All of the above cases suggest that the distinction between 2-thecous and 4-thecous anthers should be dropped for the purpose of generic delimitation. What would this mean for the system of the Lauraceae? Actually, the change would only be moderate. Some genera already comprise species with 2-thecous and with 4-thecous anthers (see above), and sometimes the number of thecae is variable within otherwise very homogeneous species (e.g., in *Urbanodendron verrucosum* (Nees) Mez, see Rohwer, 1988). In the New World only the three genera discussed above would need to be (partly) dismembered, and this would make the classification more natural. On the other hand, it would become technically more difficult, but not impossible, to describe the difference between *Ocotea* and *Aniba*. In the Old World the change would involve only a few genera, but a large number of species. *Alseodaphne* and *Dehaasia*, with together some 80–90 species, would have to be merged, and new generic definitions would have to be found in the complex formed by *Lindera*, *Litsea*, and *Actinodaphne*, with together some 600–800 species. Within this complex the involucrum enveloping whole or partial inflorescences is sometimes derived from budscales at the base of the inflorescence and sometimes from floral bracts. There are also marked differences in the inflorescence structure (Kostermans, pers. comm.), which do not parallel the 2-thecous/4-thecous distinction, but which may correspond to structurally different groups in wood and bark characters (Richter, 1981). Only the sheer size of this complex precludes an effective revision. All other genera with 2-thecous anthers, whether palaeotropical or neotropical, are either definable by additional floral or fruit characters, or their species had already been placed within a genus with 4-thecous anthers by a previous author.

OTHER GENERIC CHARACTERS

But what about the value of other characters? Are they really more reliable than the number of thecae? The answer is more complicated than the question implies. No single character has exclusively one well-defined state in every genus. Somewhere in the family we always find characters not so clearly expressed, or intermediate states, or exceptions to the prevailing state of a genus. This statement, however, is only possible because we still can define genera, as groups with a syndrome of certain characters that are constant or nearly constant for this particular group, but may be variable in other groups defined by other characters. Staminodia, for example, are consistently absent in *Rhodostemonodaphne* and consistently large and glandular in *Persea*, but in *Ocotea* they can be absent, or small and nonglandular, or small with a glandular tip, or with a relatively large apical gland. This means that on the one hand any character will be misleading when given too much emphasis, and on the other hand any character (including the number of thecae) can be useful in conjunction with others.

Especially the fruit characters deserve more attention. With few exceptions (which need further investigation) they are remarkably constant within

natural groups as defined by other, often less obvious characters. Of course, the fruit characters are not diverse enough to differentiate all genera, but when they do show a clear-cut discontinuity, this mostly warrants a generic distinction. Unfortunately, nearly all conceivable intermediates are present in the large genus *Ocotea*, which is defined only negatively, i.e., by the absence of the diagnostic characters of more distinctive genera.

A good example of the variation of important characters (including fruit characters) within a genus is found in the neotropical species of *Persea*. In *Persea* subg. *Persea* the tepals are equal, widely patent to reflexed at anthesis, and lost in fruit, whereas in subg. *Eriodaphne* they are unequal, almost erect to slightly spreading at anthesis, and persistent, indurate, and widely patent in fruit. This seems to be a better distinction than found between many genera, but the gap is bridged by a few Central American species (*P. pallida*, *P. rigens*, *P. steyermarkii*, *P. sylvatica*), and by the Asian subg. (or genus) *Machilus*. These species have the equal tepals of subg. *Persea*, but they are persistent in fruit as in subg. *Eriodaphne* (although usually not incrassate in *Machilus*). Representatives of this group also occur in Venezuela, Ecuador, and Peru, but lack of good collections has hampered their correct placement. Recently, a *Persea* from Surinam was described with yet another combination of characters. Its tepals are unequal as in *Eriodaphne*, but deciduous, as in *Persea* (van der Werff, 1989).

The number of thecae is also variable in the neotropical *Persea* species. Most commonly one finds nine 4-celled stamens, but some species have nine 2-celled stamens, six 4-celled and three 2-celled stamens, or six 4-celled stamens and the third whorl staminodial. Needless to say, our understanding of this genus is far from complete, and it is equally not clear how to differentiate *Persea* from its closest relatives, especially in Asia.

While *Machilus* and *Phoebe* are clear-cut genera in Asia, the distinction between South American *Persea* subg. *Eriodaphne* and Asian *Phoebe* can be difficult. As mentioned above, the tepals are unequal and more or less patent in fruit in the former group, whereas in the latter they are (nearly) equal and erect. However, in some species of subg. *Eriodaphne* the "slightly unequal" tepals are less different from each other than the "nearly equal" tepals in some species of *Phoebe*, and in some species (e.g., *Persea cuneata* Meissn., see fig. 3 in Kopp, 1966) they can be nearly erect. If *P. cuneata* was an Old World species, it would be placed in *Phoebe* without much hesitation, or in *Apollonias*, if this is kept separate from *Phoebe*, based on its 2-thecous anthers.

What can we expect from future studies on neotropical Lauraceae? As more and better collections become available, the number of species will increase and the distribution of the taxa will become better known. Some of the new species will possess such unusual combinations of characters that additional genera will have to be described. Two genera have recently been described, *Williamodendron* (Kubitzki & Richter, 1987), initially only known from Amazonian Brazil, northern Colombia, and Costa Rica, but now also known from Peru and southern Brazil, and *Povedadaphne* (Burger, 1988), only known from Costa Rica. We have mentioned earlier several taxa that probably represent additional genera. We estimate that 25–35% of the neotropical species of Lauraceae have not yet been described, and even under optimum conditions, collecting plus descriptive studies would require at least a decade before an inventory of neotropical Lauraceae will be reasonably complete.

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GAMANTHERA (LAURACEAE), A NEW GENUS FROM COSTA RICA[1]

Henk van der Werff[2] *and Peter K. Endress*[3]

ABSTRACT

A new genus of the Lauraceae, *Gamanthera*, is described from Costa Rica. It is distinguished from all other Lauraceae by its completely fused stamens, forming a synandrium, with only three, two, or one locellus, and by its monoecious nature.

During the past few years, intensive collecting efforts in Costa Rica have resulted in a great number of additions to the *Flora Costaricensis*, as well as in a number of undescribed taxa. Several new species of Lauraceae have recently been published (Hammel, 1986; Burger, 1988; van der Werff, 1988; Zamora et al., 1988), and 14 species were published in the treatment of the Lauraceae for the *Flora Costaricensis* (Burger & van der Werff, 1990). Burger (1988) published a new genus, *Povedadaphne*, from Costa Rica and noted that recently five mostly South American genera had been added to the known flora of Costa Rica. Recent fieldwork organized under the auspices of the Manual Flora of Costa Rica project, organized by the Missouri Botanical Garden, has yielded another Lauracea from Costa Rica, which is here described as a new, monotypic genus. The surge of new taxa of Lauraceae from Costa Rica can be attributed to the unusual richness of its flora, but perhaps a more likely explanation for these discoveries is the excellence of the Costa Rican botanists participating in the botanical exploration of their country. It is, therefore, with pleasure that we name the new species after Gerardo Herrera, who discovered it and whose excellent collections of Lauraceae have given us much pleasure to work with.

Gamanthera herrerae van der Werff, gen. et sp. nov. TYPE: Costa Rica. Alajuela, Upala, Colonia Puntarenas, along Río Chimuria, tree, 8 m, flowers yellowish, fruits green, cupule pink, 11 Nov. 1987, *Herrera 1228* (holotype, MO; isotypes, BM, CR, HBG, US). Figure 1.

Arbores monoeciae. Folia alterna, venatione pinnata. Gemmae conspicue bracteatae. Inflorescentiae axillares, paniculatae, basi bracteis vel cicatricibus bractearum praeditae, ex floribus solum masculinis vel femineis constantes. Flores masculini synandrio tribus staminibus perfecte connatis facto. Synandrium 3, 2, vel 1-locellatum. Fructus cupulae duplimarginatae insidens.

Tree, 8 m tall. Twigs terete, densely brown-tomentellous, with occasional whorls of scars from fallen bracts. Axillary and terminal buds conspicuous, covered by several whorls of bracts, the small basal bracts brown-pubescent outside, the large inner bracts glabrous or nearly so, but with ciliate margins; inner surface of bracts glabrous. Leaves alternate, chartaceous, 12–20 × 5–8 cm, elliptic, margin undulate, the base cuneate to broadly cuneate, the apex shortly acuminate, the acumen to ca. 1 cm long; upper surface of mature leaves with midrib tomentellous, especially near the base, otherwise glabrous, young leaves with a rather dense indument of short (0.2–0.3 mm), erect hairs; lower surface with midrib and lateral veins brown-tomentellous, the lamina with erect pubescence, hairs ca. 0.3 mm long; lateral veins 5–8 on each side, arching upward near the margin, not or very weakly loop-connected, venation immersed or nearly so on upper surface, midrib and lateral veins prominently raised on lower surface, tertiary venation also raised. Petioles terete, brown-tomentellous, 1–1.5 cm (rarely to 2 cm) long, adaxially flattened, abaxially terete. Inflorescences axillary, brown-tomentose, paniculate, to 7 cm long, with bracts or scars of fallen bracts at the base, flowers clustered near the tips of the secondary or very short tertiary axes, rarely solitary, not cymosely arranged; axes

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FIGURE 1. *Gamanthera herrerae*.—A. Habit.—B. Flower.—C. Young and old fruits, the young ones enclosed in the cupule, the old one exserted.—D. Detail of inflorescence.—E. Base of leaf, showing indument.—F. Detail of stem, showing linear scars from fallen bracts and circular scars from fallen buds.—G. Base of axillary inflorescence, showing linear scars from fallen bracts.

and flowers subtended by bracts, these broadly to narrowly ovate-elliptic, to 2.5 mm long or, when fallen off, by a scar. Inflorescences with either staminate or pistillate flowers. Flowers sessile or nearly so, unisexual, 4–4.5 mm long, including the narrowed base; staminate and pistillate flowers externally very similar; tepals 6, erect, broadly triangular, pubescent outside, the free part to 1.5

mm long, inner 3 tepals shorter than outer 3. Staminate flowers with a central, narrowly conical synandrium formed by fusion of 3 stamens (Fig. 2), the fusion complete and individual stamens not recognizable, the synandrium 2 mm long, the glabrous anther-bearing part and the densely pubescent fused filaments each 1 mm long; locelli 3, 2, or infrequently 1; staminodia and pistillode lacking. Pollen grains globose, inaperturate, spinulose (Fig. 3). Bisexual flowers with a one-sided(?) synandrium; ovary situated beside(?) the synandrium, glabrous, narrowly ellipsoid, gradually narrowed into a slender, long style (Fig. 4). Receptacle glabrous inside. Stigma not seen. Fruit ellipsoid, ca. 1.5 cm long, the exserted part 1 cm long, cupule deeply cupshaped, double-rimmed, the undulate-lobed outer margin strongly reflexed.

Paratype. Collected from same tree as type specimen, *Grayum et al. 9039* (CR, F, LE, MEXU, MO, S, USJ, Z).

Anatomy of the Staminate Flower

MATERIAL AND METHODS

Figures 5 and 6 were prepared by P. Endress. Pickled flowers of the collection *Grayum 9039* were examined with the scanning electron microscope (SEM) after critical point drying and sputter coating with Au/Pd. Other samples were used for microtome serial sections and stained with safranin and astra blue. Figures 2–4 were prepared by H. van der Werff. Dried flowers were dissected without rehydration and sputter coated with Au.

RESULTS

The perianth consists of two trimerous whorls of tepals (Fig. 8). The androecium in the center of the flower consists of a massive conical body which bears one to three pollen sacs at its top (Figs. 7, 9, 10, 11). Nectaries are lacking. At anthesis the flower does not expand and retains the globular shape of the bud (Fig. 5). Only the upper part of the androecium with the pollen sacs protrudes through the small opening of the flower and is exposed (Fig. 6). Each pollen sac opens by a flap, which is hinged at the top and recurves toward the top (Figs. 5, 6). The flap is shorter than the pollen sac and does not extend to its base (Fig. 11C). The diagrammatic position of the pollen sacs is opposite the inner tepals (Fig. 8). The androecium is always served by three collateral vascular bundles irrespective of the number of pollen sacs (Fig. 11A–C). In androecia with three pollen sacs the vascular bundles alternate with the pollen sacs (Fig. 11C). The bundles are situated toward the center of the androecium and terminate somewhat above the lower end of the pollen sacs (Fig. 11C).

DISCUSSION—INTERPRETATION OF THE ANDROECIUM

How is this highly unusual androecium to be interpreted? Normal stamens of Lauraceae are served by a single vascular bundle situated in the center of the stamen behind the two pollen sacs (if the anther is bilocular), as seen in a transverse section. Here, in *Grayum 9039*, there are three vascular bundles, which suggest three stamens. The three vascular bundles alternate with the tepals of the inner whorl. In lauraceous taxa, where the androecium is reduced to a single whorl, e.g., in *Licaria* (cf. Mez, 1889, as *Misanteca*; Kostermans, 1957) or *Mezilaurus* (van der Werff, 1987), the stamens alternate with the tepals of the inner whorl.

From this it follows that the conical androecium consists of three stamens that are completely congenitally fused into a compact synandrium. If three pollen sacs are differentiated, each "anther" consists of two "half" pollen sacs in that the two neighboring pollen sacs of two stamens have merged into one. Merger of two pollen sacs of different thecae (or at least of their flaps) into one functional unit also occasionally occurs in other lauralian groups; e.g., in *Siparuna* the two flaps of an anther may merge into one (here, two thecae of the same anther) (cf. Endress & Hufford, 1989).

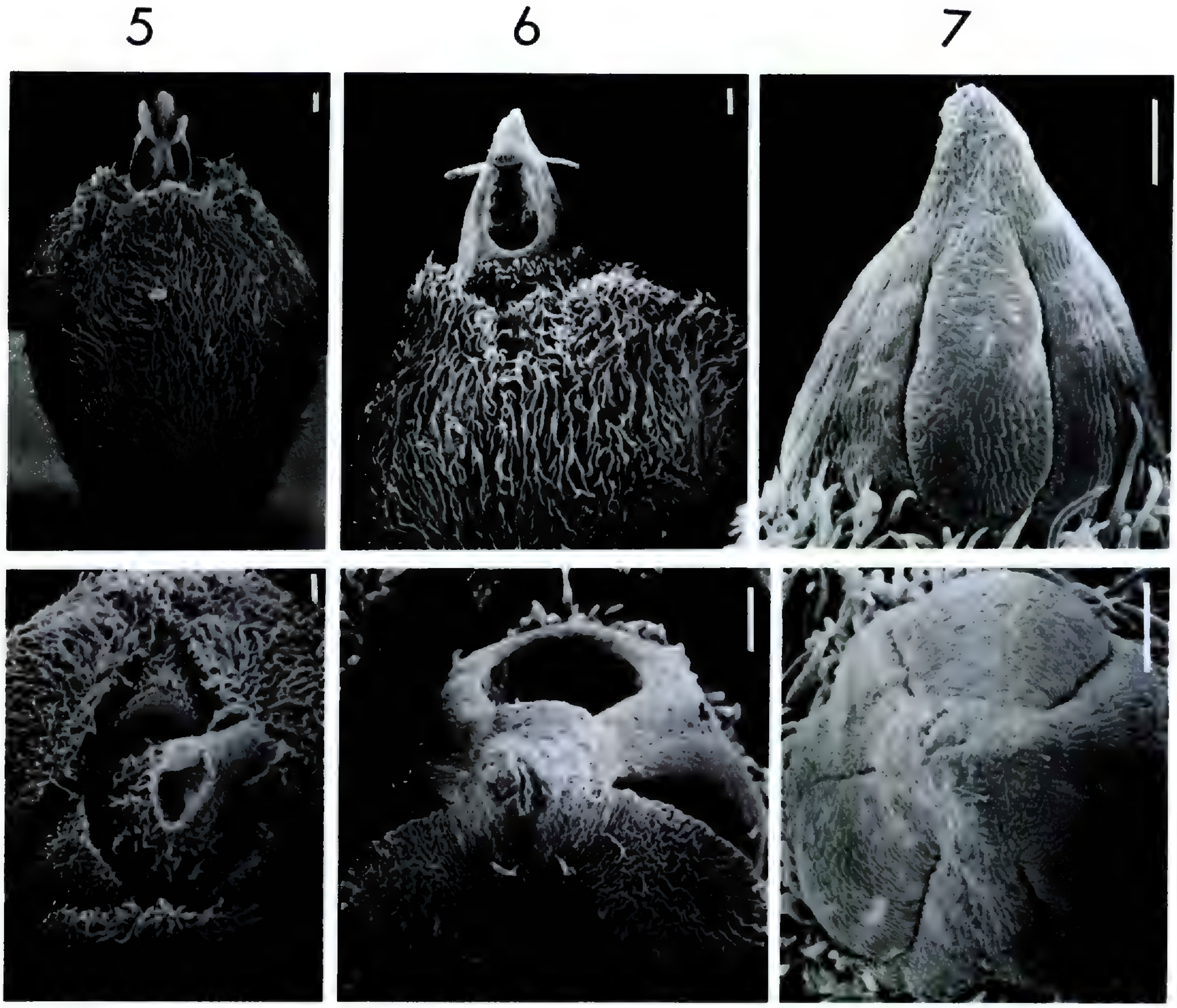
The male flowers of *Grayum 9039*, therefore, represent an extremely reduced stage previously unknown in the Lauraceae. In other taxa with bisexual flowers reduction of the androecium to one stamen whorl, which is congenitally fused into a tube surrounding the gynoecium, is the ultimate stage so far known. This is the case in species of *Licaria* (Kostermans, 1957; as *Misanteca* in Mez, 1889) and *Mezilaurus* (van der Werff, 1987). In *Kubitzkia* there are still three staminal whorls, whereby the third is connate into a tube (as *Systemonodaphne* in Kostermans, 1957). Fusion of the filaments of whorls II and III occurs in an undescribed species of *Rhodostemonodaphne* (van der Werff, pers. obs.). However, the anthers remain free in all of these cases.

In *Grayum 9039*, congenital fusion of the remaining three stamens into a massive (compact) central body and fusion of neighboring pollen sacs of neighboring stamens, reduction of pollen sac

fig.2

fig.4

fig.3



FIGURES 5–10. SEM micrographs of flowers and pollen of *Grayum 9039*. Scale bars = 0.1 mm.—5. Open flower from the side, two open pollen sacs visible.—6. Upper half of open flower, three open pollen sacs visible—7. Synandrium from the side, three closed pollen sacs with the dehiscence lines of the flaps visible.—8. Open flower from above, the six tepals and the synandrium with the three open pollen sacs visible.—9. Synandrium from above, three open pollen sacs visible; the flap of the uppermost pollen sac has been removed.—10. Synandrium from above, three closed pollen sacs visible.

number to two or one in some flowers, and loss of the nectary appendages, represent a further step in this trend of reduction within the Lauraceae.

Synandry is relatively frequent in Magnoliidae. Because the shape of the stamens is more or less bulky, synandry is relatively easy to establish from a morphogenetical point of view, mainly in unisexual flowers, where a gynoecium is lacking as a potential obstacle in the floral center (Endress, 1989).

DISCUSSION

Gamanthera herrerae is currently known only from the vicinity of Upala in the Alajuela Province, Costa Rica. The two collections were made in con-

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FIGURES 2–4. SEM micrographs of flowers and pollen of *Grayum 9039*.—2. Dissected male flower, showing the synandrium.—3. Pollen grain.—4. Dissected female flower, showing glabrous ovary below the synandrium and the slender style; part of the synandrium removed to show style. Scale bars in Figures 2 and 4 = 0.5 mm; in Figure 3 = 0.005 mm.

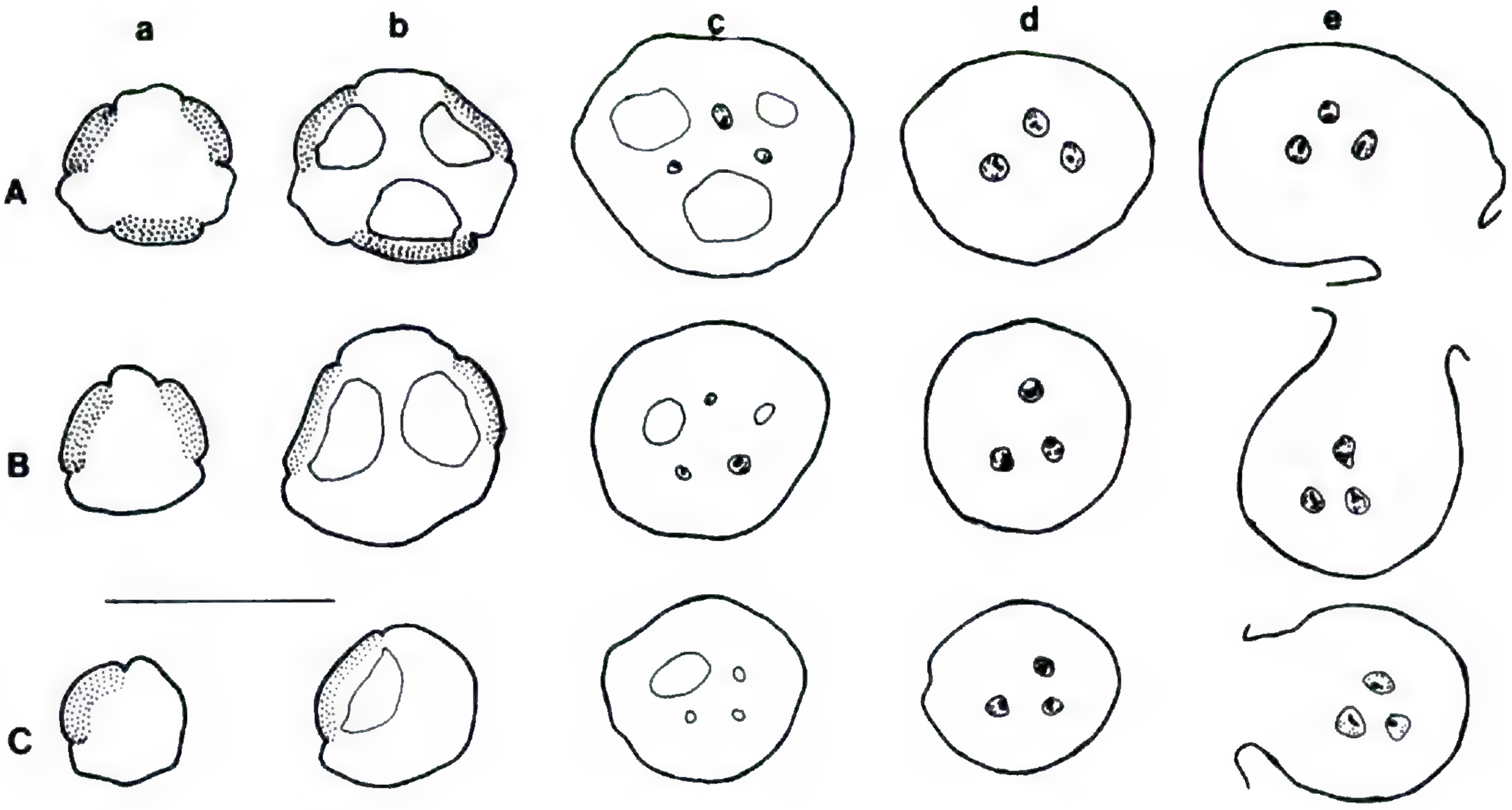

FIGURE 11. Microtome serial transverse sections of synandria of three male flowers of *Grayum 9039*. Scale bar = 0.5 mm. Endothecium of the pollen sacs stippled. In vascular bundles xylem black, phloem stippled.—A. Synandrium with three pollen sacs.—B. Synandrium with two pollen sacs.—C. Synandrium with one pollen sac. (a) Sections at upper end of pollen sacs. (b) Sections at middle level of pollen sacs. (c) Sections at base of pollen sacs. (d) Sections below pollen sacs. (e) Sections at base of synandrium.

secutive years from the same tree. A search in the vicinity yielded only two additional trees, one sterile, the other juvenile. The trees were not large, but hard to find; it is likely that, if one would be willing to spend a week searching, more trees could be located.

Several inflorescences contain deformed flowers infested by insect larvae. Such flowers have basal, spreading tepals and a central, depressed-globose, densely pubescent growth. This growth probably represents the deformed synandrium, as is indicated by the densely pubescent surface. The locelli-bearing part of the synandrium is usually present, but always more or less lateral, never at the tip of the growth. The deformed flowers have a hollow center, which usually contain an insect larva. Such flowers were only found in the male inflorescences and never contained a trace of an ovary. Infructescences with "young fruits" are part of all specimens. These "young fruits" are almost completely included in a broad, flat-topped cupule (the two righthand "fruits" in Fig. 1C). Upon dissection these "fruits" show an absence of a well-defined outer wall and a seed; instead they are filled with nondifferentiated tissue which contains a few, irregular cavities. Although we did not find larvae in these "fruits," we consider them abnormalities, probably caused by insect or mite activity. The lefthand fruit in Figure 1C is not abnormal; it has the distinct outer wall found in other Lauraceae and contains a shrivelled, dried seed. The two collections of *Gamanthera* include only one normal fruit but several dozen of the abnormal "young fruits."

This new genus possesses several features that are either unknown or very rare in neotropical Lauraceae. The most striking of these is the androecium, which consists of three completely fused stamens, as is described above. Staminodia have not been found, nor are there glands associated with the synandrium. A complete fusion of stamens, including anthers, has not previously been reported for Lauraceae. This synandrium, which is located in the center of the flower, appears to be a single stamen and only a study of the vascularization showed its true origin. The number of locelli on the synandrium can be three, two, or one; one synandrium with four locelli was found with the locelli arranged in two horizontal pairs, the septum separating the two locelli of one pair much thinner than the walls separating the pairs.

A second unique feature in *Gamanthera* (at least for Lauraceae) is the presence of two flower types on the same tree. Lauraceae have either bisexual or unisexual flowers; if unisexual flowers are present, the species are dioecious. In most cases, the unisexual character of the flowers can be readily seen, but in some species (for instance, in *Ocotea*,

van der Werff, pers. obs.) the reduction of the nonfunctional organs in the flower is not obvious, and it can be difficult to decide whether flowers are unisexual or bisexual. Howard (1981) reported that some species of *Ocotea* s.l. were found to be polygamodioecious, with perfect and functionally unisexual flowers present in the same inflorescence, an observation we have not been able to confirm. The first collection of *Gamanthera* included inflorescences and young fruits, sometimes with the inflorescence and fruit attached to the same twig. The inflorescences consisted of only staminate flowers, without even a trace of a gynoecium. After much searching, pistillate flowers were found on the infructescences as old, dried flowers. Seven flowers of different infructescences were dissected and these were all pistillate. The pistillate flowers are, without dissection, indistinguishable from the staminate flowers and possess a similar synandrium. The synandrium often persists on young fruits. We did not find pollen grains in the synandria of the pistillate flowers, but have not found pollen grains in synandria with opened valves of staminate flowers either. Pollen was only found in flowers with the synandrium still included in the flower and valves closed. Thus, it is possible that the flowers described as pistillate are bisexual and that *Gamanthera* has unisexual (staminate) and bisexual flowers on separate inflorescences on the same plant, rather than pistillate and staminate flowers on separate inflorescences on the same plant. Either way, this is a situation not previously recorded for Lauraceae. It is not yet clear how pollinization takes place. In the pistillate flowers the ovary is fully covered by the synandrium. In contrast to the staminate flowers, the synandrium of the pistillate flowers is hollow and the style ascends through the hollow core (Fig. 4). The style can be followed up to the level of the locelli, where it seems to disappear. A pore in the synandrium through which a stigma can penetrate has not been found. Such a pore is likely present in younger flowers, but might become unrecognizable in old flowers. The pistillate flowers seen are only present on infructescences and are likely several months old. On the twig that carries a staminate inflorescence and an infructescence, the infructescence is attached much lower on the twig than the inflorescence. In *Gamanthera* it is difficult to estimate the age of the flowers, as there are, apart from the elongation of the synandrium, no changes in size or shape. The general trend in Lauraceae is that staminate flowers fall off soon after shedding their pollen. Because young staminate flowers (in which synandria are still enclosed in the flowers and locelli have not opened) are present on some specimens, the staminate flowers are probably not very old. On the other hand, the development of the cupules on the infructescences suggests that these pistillate inflorescences are much older. Therefore, it seems likely that the pistillate and staminate flowers on the available specimens have quite different ages, and it is not certain that staminate and pistillate flowers are simultaneously functional on the same tree. If this is not the case, *Gamanthera* could be an interesting example of dichogamy in a monoecious species with unisexual flowers. Dichogamy has been reported for Lauraceae in genera with perfect flowers (Stout, 1927; Kubitzki & Kurz, 1984) and seems widespread in the family.

A third interesting feature of *Gamanthera* is the series of bracts surrounding the inflorescence and vegetative buds. Once inflorescences and twigs grow out of the buds, the bracts fall off and leave clusters of linear scars at the base of the inflorescence and young twigs. Clusters of scars on twigs occur in several genera of neotropical Lauraceae (*Aniba*, *Endlicheria*, *Mezilaurus*, *Pleurothyrium*, van der Werff, pers. obs.). Species in these genera with bracts all have leaves clustered near the tips of their branches, and the bracts are narrowly elliptic with an acute tip and frequently with a rudimentary midrib, quite unlike the broad, scalelike bracts found in *Gamanthera*. In *Persea schiedeana*, another species with clustered leaves, the bracts surrounding the vegetative buds are broad and scalelike, but this species lacks bracts at the base of the inflorescences. The only genus in the Neotropics with scalelike bracts surrounding the vegetative buds and with alternate leaves (apart from *Gamanthera*) is *Litsea*, which occurs at high elevations from Mexico to Costa Rica. In *Litsea* the flowers are arranged in pseudo-umbels, which are subtended by scalelike bracts. It is likely that these bracts represent the floral bracts, which, like the flowers, have become greatly condensed. In *Gamanthera*, floral bracts are present in addition to the bracts at the base of the inflorescence, and these latter bracts seem unique among neotropical Lauraceae.

RELATIONSHIPS

Infrafamilial classification of Lauraceae (Kostermans, 1957; Hutchinson, 1964) is based on the following characters: presence or absence of bracts (or decussate bracts surrounding the subumbellate inflorescences), development of cupule, number of fertile stamens, and number of anther cells. The characters found in *Gamanthera* do not agree with

any of the tribes as defined by these authors. Monoecious trees with inflorescences composed of flowers of one sex only had not been reported before in Lauraceae. The bracts at the base of the inflorescences suggest a relationship with the Laureae, but against this argue the facts that in the Laureae the bracts subtend the (mostly subumbellate) flowers, not the common peduncle, as in *Gamanthera*; that in the Laureae inflorescences are subumbellate or racemose, not paniculate as in *Gamanthera*; and that in Laureae the cupule is never double-margined. The other tribes are defined by cupule and androecial characters. The highly reduced androecium of *Gamanthera* precludes placement in any of these tribes. Probably the closest is the subtribe Anibineae of Kostermans (1957), which includes genera with double-margined cupules and some fusion of stamens (but never to the degree found in *Gamanthera*). Against the placement of *Gamanthera* in the Anibineae are the bracts surrounding the inflorescences and vegetative buds, and the monoecious condition. In favor of a relationship with Anibineae are the fact that Anibineae are well represented in the Neotropics, whereas Laureae include only one neotropical species.

The pollen of *Gamanthera* (Fig. 3) is globose, inaperturate, and spinulose, and agrees with the general pollen characteristics of neotropical Lauraceae (Raj & van der Werff, 1988). Diameter of the grains is about 20 μ and the spinules are seated on cushionlike bases, these without granular processes. These characters agree well with the Anibineae and do not indicate a relationship with the Laureae.

H. G. Richter (pers. comm.) reported that the wood of *Gamanthera* is nondescript and typical of Lauraceae; the bark corresponds with Richter's (1981) *Licaria* type 1, *Aniba*, and *Ocotea* pro parte. These conclusions rule out a relationship of *Gamanthera* with the Laureae and place it somewhere in the Anibineae. A close relationship with *Mezilaurus*, which includes some species with fused filaments of the three stamens, is not likely because *Mezilaurus* differs in its wood characters (Richter, 1981), clustered leaves, and small, platelike cupules. Instead, *Gamanthera* might be closer related to *Licaria*, although we consider *Gamanthera* distinct from *Licaria* because of its synandrium and clusters of bracts along twigs and at base of inflorescences. The relationships between genera of Lauraceae are presently not well understood and are in need of much further study.

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NEW SPECIES OF LAURACEAE FROM ECUADOR AND PERU[1]

Henk van der Werff[2]

ABSTRACT

Seven species of Lauraceae from Ecuador and Peru are described and their affinities are discussed. The new species belong to the genera *Caryodaphnopsis* (*C. tomentosa*), *Cinnamomum* (*C. napoense* and *C. palaciosii*), *Endlicheria* (*E. citriodora*), *Ocotea* (*O. alata*, *O. infrafoveolata*, and *O. rotundata*), and *Rhodostemonodaphne* (*R. synandra*).

Intensive fieldwork during the past few years in Peru (by A. Gentry, R. Vásquez, and N. Jaramillo) and Ecuador (mostly by D. Neill, C. Cerón, and W. Palacios) has resulted in a large number of excellent collections of Lauraceae. Several of these represent undescribed species and seven of the most striking ones are described in this contribution. I expect that as long as these collecting efforts continue, more undescribed species will become known and articles such as this one, describing these novelties, will appear with some regularity.

Caryodaphnopsis tomentosa van der Werff, sp. nov. TYPE: Ecuador. Napo, Estación Biológica Jatun Sacha, tree, 25 m tall, flowers green, 7 Aug. 1989, *Palacios 4337* (holotype, MO; isotypes, AAU, BOG, CR, F, GH, HBG, K, KUN, L, LE, QAME, QCE, QRS, NY, P, S, US). Figure 1.

Ab speciebus ceteris Caryodaphnopsis ramulis et foliis subtus tomentosis, staminibus fertilibus 6, bilocellatis, recedit.

Tree, 25 m tall, the trunk with buttresses 1 m high. Twigs terete or slightly quadrangular, brown-tomentose when young, becoming glabrous. Terminal bud brown-tomentose. Leaves opposite, coriaceous, 8–18 × 3–7 cm, elliptic, the base obtuse or acute, the tip acute, triveined, the 2 lateral veins beginning at the very leaf base and ending in the apex, impressed on the upper surface and prominently raised on the lower surface, the perpendicular tertiary veins raised on the lower surface, the lateral veins with up to 10 branchlets toward the margin, these strongly arching upward and loop-connected; lamina glabrous above or with traces of pubescence at the bases of the major veins, brown-tomentose on lower surface. Petioles to 1 cm long, tomentose. Inflorescences clustered in the axils of leaves, paniculate, with opposite or alternate branching, to 7 cm long, whitish tomentellous in sicco, flowers grouped in cymes. Bracts of inflorescences persistent, linear, the larger ones ca. 2 mm long, bracts subtending flowers only half as long. Pedicels 2–3 mm long. Flowers green, without odor (fide collector). Tepals 6, strongly unequal, the outer three broadly ovate to roundfish, ca. 1 mm long, pubescent outside, glabrous inside, spreading; inner tepals erect, ca. 3 mm long, elliptic, pubescent outside, inside with some scattered hairs mostly near the margin. Stamens of whorls I and II fertile, 2-celled, 1.5 mm long, the filament 1 mm long, dorsally pubescent, otherwise glabrous; stamens of whorl III 0.7 mm long, sterile or with 2 minute, vestigial locelli, the filament with two basal glands, the anther well developed and clearly differentiated from the filament; staminodia (whorl IV) ca. 0.7 mm long, with a pubescent filament and glabrous, cordate tip. Ovary glabrous, ellipsoid, gradually narrowed into the slender style. Receptacle shallow, pubescent inside.

Caryodaphnopsis tomentosa is a very distinctive species by virtue of its tomentose pubescence on twigs and leaves, its pubescent inflorescences and flowers, the presence of only six fertile two-celled stamens, and its coriaceous leaves with strongly raised venation. Although its androecium is unique in *Caryodaphnopsis*, it possesses all other characters of the genus, such as opposite leaves, strongly unequal tepals, and a long, slender style.

[1] Luther Raechal kindly photographed the type specimens. Drawings were made by John Myers. I thank the National Geographic Society for financial support of fieldwork in Peru and Ecuador (grant numbers 3480-86 and 3821-88).

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FIGURE 1. *Caryodaphnopsis tomentosa*.—A. Habit.—B. Detail of inflorescence.—C. Pistil.—D. Stamen of whorl III (sterile).—E. Staminode of whorl IV.—F. Stamen of whorl I/II ventral view.—G. Larva inside flower.

Although *Caryodaphnopsis tomentosa* is only known with certainty from the type collection, three sterile collections from Peru probably represent the same species. These are: *Gentry et al. 42762* (MO) and *Vásquez & Jaramillo 6387* (MO), both from Yanamono, Explorama Tourist Camp, Maynas, Loreto, and *Gentry et al. 55831* (MO), from the Explorama Inn, Maynas, Loreto. In venation and indument these collections are a good match for the type collection.

Although fruits have not yet been collected, they were described by the collector as small and round, a fruit type which is to be expected in this group of *Caryodaphnopsis* species with strongly triveined leaves (van der Werff, 1988). The collector noted that small white larvae were frequently present in the flowers and, indeed, larvae were found in most dissected flowers.

Cinnamomum Schaeffer

The group of species to which *Cinnamomum napoense* and *C. palaciosii* belong has been included in *Phoebe* by earlier authors (Mez, 1889, for instance). Because Mez was the last person to survey all neotropical Lauraceae, his concepts of species and genera have long remained unchallenged. Until now I have, with some hesitation, accepted Mez's concept (van der Werff, 1987, 1988). Kostermans (1961) argued for the transfer of neotropical *Phoebe* species to *Cinnamomum* and made the necessary new combinations. Because various neotropical species of other genera have been erroneously described in *Phoebe*, I felt that these problems needed to be sorted out before accepting the remaining species in *Cinnamomum*. I have now changed my mind on this; it makes no sense to describe new species in a genus to which they do not belong. Although the problems with the delimitation of *Cinnamomum* are not solved and generic concepts may change again in the future, I think the neotropical species formerly treated in *Phoebe* are, with some exceptions, more closely related to *Cinnamomum* than to any other genus, and I accept *Cinnamomum* as their generic name. Wood anatomical characters also support the transfer of neotropical *Phoebe* species to *Cinnamomum* (Richter, 1981).

The neotropical *Cinnamomum* species have two areas of species richness: northern Central America and southern Brazil. The genus is poorly represented in other neotropical areas. Most collections from northern South America belong to the *C. cinnamomifolia* complex, which usually occurs in montane habitats (mostly 1,200–2,000 m). Although Mez (1889) reported the genus from Colombia and Peru, it has apparently not been recorded from Ecuador. Recent fieldwork has shown that it is represented by at least three, and probably more species in Ecuador. Further collecting may demonstrate that the paucity of known *Cinnamomum* species in northern South America reflects incomplete collecting and that the genus is represented by more species than previously thought.

A possibly useful character in the identification of *Cinnamomum* is the odor of the flowers. The species of *Cinnamomum* I have collected (*C. costaricanum* (Mez & Pitt.) Kostermans, *C. cinnamomifolium* (HBK) Kostermans s.l. in Venezuela and Ecuador, and *C. palaciosii* van der Werff) all had flowers with a similar odor of urine. As a rule, Lauraceae have pleasantly fragrant flowers, and therefore I think this peculiar odor is indicative for the neotropical *Cinnamomum* species.

Cinnamomum napoense van der Werff, sp. nov. TYPE: Ecuador. Napo, Estación Biológica Jatun Sacha, tree, 7 m, 2–5 Sep. 1988 (fl), *Palacios 2886* (holotype, MO; isotypes, QCE, QAME, AAU, HBG, NY, US). Figures 2B, 3A–F.

Ab ceteris speciebus subgeneris Heterantherae Mez foliis majoribus, petiolis longioribus et costarum axillis subtus non-barbellatis differt.

Trees, to 15 m tall. Twigs terete, glabrous or minutely puberulous when young, with a soft pith and sometimes fistulose. Terminal bud densely puberulous. Leaves alternate, somewhat clustered near the tips of branches, chartaceous, 18–30 × 6–12 cm, elliptic, the base acute or rarely obtuse, the tip acute, upper surface glabrous, lower surface glabrous and densely gland-dotted, sometimes with minute, appressed hairs along the major veins, lateral veins 5–8 on each side, arching upward near the margin and somewhat loop-connected in the upper ¼ of the leaf, midrib and lateral veins impressed on upper surface and prominently raised on lower surface, the tertiary venation less raised and drying lighter than the lamina. Basal lateral veins stronger developed than the upper ones. Tufts of hair absent from the axils of the lateral veins. Petioles glabrous, canaliculate, 3–4.5 cm long. Inflorescences clustered on very short, leafless shoots in the axils of normal leaves or along the twigs, minutely puberulous, 5–15 cm long, paniculate, the ultimate division(s) usually cymose, but occasionally racemose. Flowers yellow, pedicels 3–4 mm long. Tepals 6, erect at anthesis, ovate, 1.5–2 mm long, on both surfaces with some appressed hairs, united at the base and falling off together

FIGURE 2.—A. *Cinnamomum palaciosii.* —B.*Cinnamomum napoense.*—C.*Endlicheria citriodora.*—D. *Ocotea alata.*

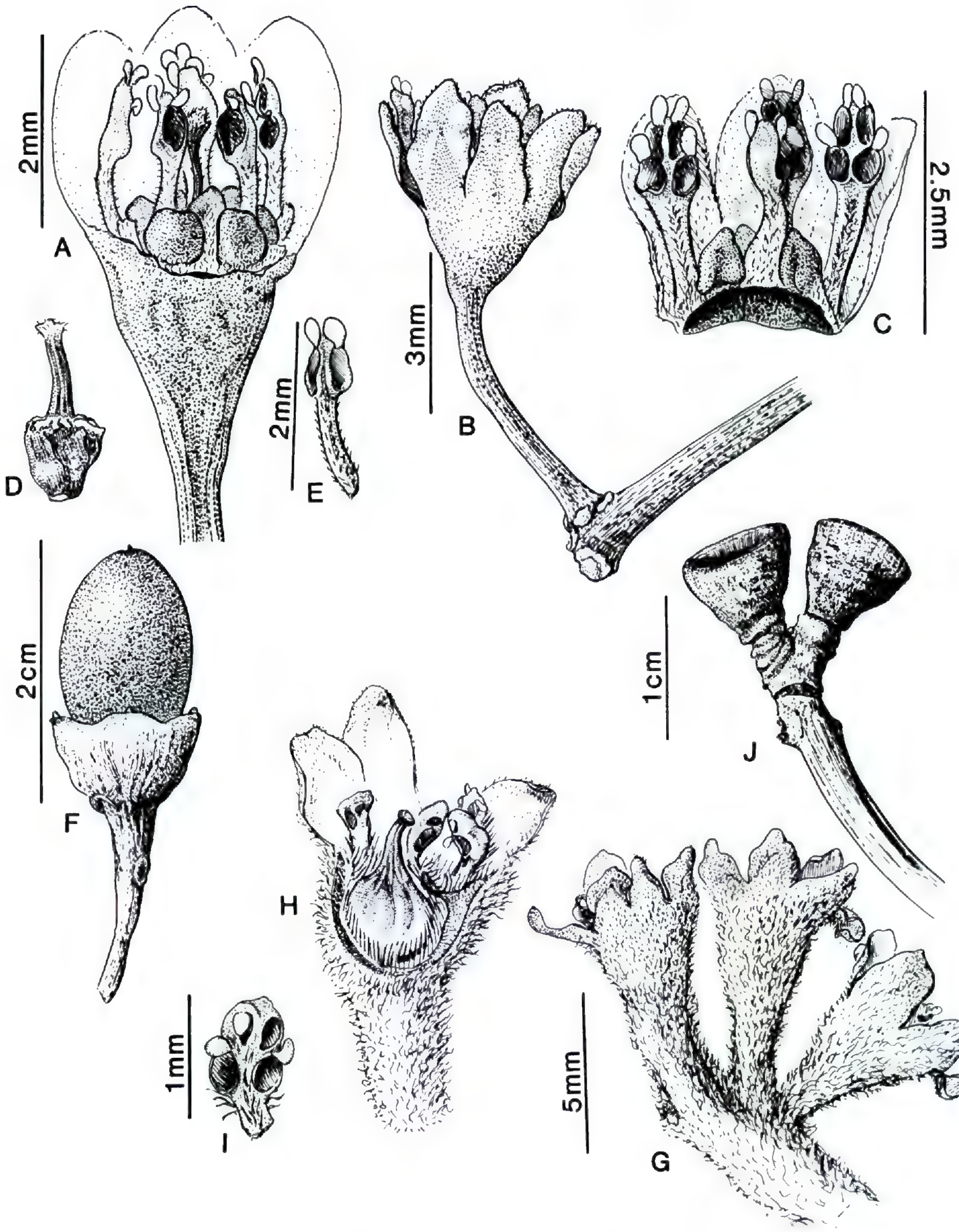

FIGURE 3. A–F. *Cinnamomum napoense*.—A. Floral detail.—B. Flower, outside.—C. Three fallen tepals, with 4-celled stamens of whorl I/II, a 2-celled stamen of whorl III with basal glands and a staminode.—D. Pistil.—E. Stamen of whorl III, the basal glands lacking, dorsal view.—F. Cupule with fruit. G–J. *Ocotea rotundata*.—G. Part of inflorescence.—H. Flower with several tepals removed.—I. Stamen of whorl I/II, ventral view.—J. Cupules.

with the stamens in old flowers. Stamens 9, the outer six 4-celled, attached near the base of the tepals and slightly shorter than them, anthers ca. 0.8 mm long, cells opening introrsely and arranged in 2 horizontal pairs, the filament gradually widened into the anther, with some short hairs, especially dorsally; the inner 3 and staminodia attached on a ridge which is bent inward and largely covers the ovary, inner 3 stamens 2-celled, slightly shorter than the stamens of the outer whorls, the cells opening extrorsely, the sparsely pubescent filament about as long as the anther; glands small, attached at the base of the stamens of the whorl III; staminodia 3, ca. 0.6 mm long, with a very short, pubescent filament and a large, sagittate tip. Ovary glabrous, ellipsoid, included in the receptacle, style slender, about as long as the ovary, the entire pistil ca. 1.8 mm long; receptacle with scattered hairs inside. Cupule ca. 1 cm tall, the rim slightly lobed, the young fruit included, older fruits greatly exserted,

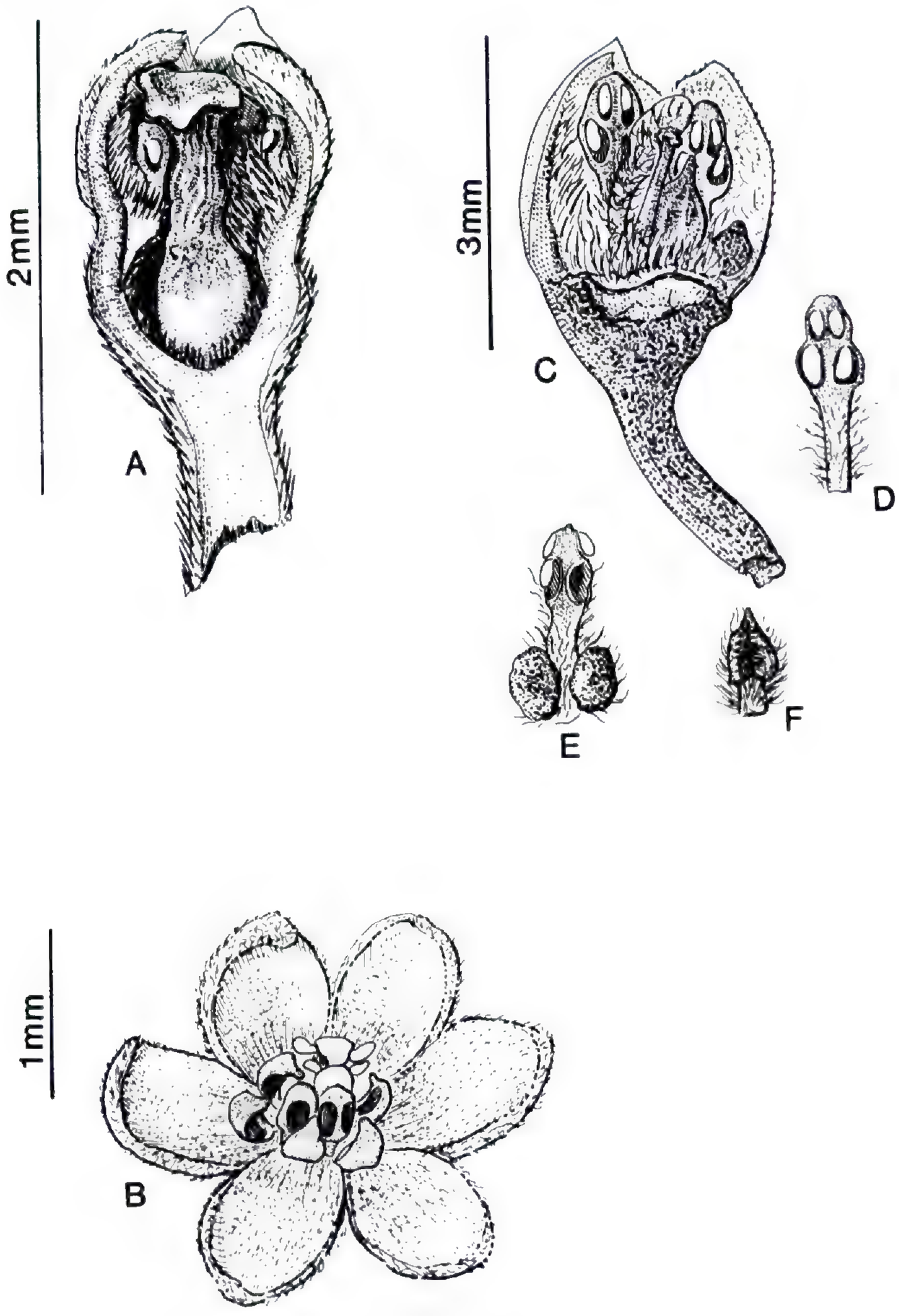

FIGURE 4. A, B. *Endlicheria citriodora.*—A. Cross section through pistillate flower.—B. Staminate flower. C–F. *Cinnamomum palaciosii.*—C. Flower, with some tepals removed.—D. Stamen of whorl I/II, ventral view.—E. Stamen of whorl III, dorsal view.—F. Staminode of whorl IV.

ca. 2 cm long; margin of cupule often with remnants of stamens.

Paratypes. ECUADOR, NAPO: Río Wai si ayá, *Brandbyge et al. 36207* (fl) (AAU); San Pablo de los Secoyas, *Brandbyge et al. 36229* (fl) (AAU); km 32 carretera Hollin-Loreto, *Neill et al. 8605*, (fl) (MO, QAME); Reserva Biológica Jatun Sacha, *Palacios 1316* (fl) (MO, QAME), *4396* (MO, QAME), *Cerón 5970* (fr) (MO, QAME); Río Napo, 8 km from Pto. Misahualli, *Palacios 2979* (fl) (MO, QAME); Añangu, *SEF 8807* (fr) (NY); Reserva Floristica El Chuncho, *Zaruma 611* (MO, QAME).

Flowers: August–September; fruits (mature): January. By virtue of its 2-celled anthers of the whorl III of stamens, *Cinnamomum napoense* belongs to subg. *Heteranthera* Mez. This subgenus consists of two Peruvian and several Brazilian species. The Brazilian species differ in their smaller leaves (less than 10 cm long), shorter petioles (less than 15 mm long) and often dense pubescence on the lower side of the leaves. Of the two Peruvian species, *C. subsessile* (Meissner) Kostermans has subsessile leaves with a cordate base and *C. heteranthera* (R. & P.) Kostermans has small (to 9 cm long) leaves with tufts of hair in the axils of the lateral veins. Thus, *C. napoense* differs from the other species of subg. *Heteranthera* by its large leaves, long petioles, and lack of axillary tufts of hair. In older flowers the tepals break off just above their base and the margin of the cupule is slightly undulating due to the presence of the short tepal bases. Often a few stamens also persist on the margin of the cupule.

Cinnamomum palaciosii van der Werff, sp. nov. TYPE: Ecuador. Imbabura: forest remnant along road Apuela-Otovalo near Apuela, elev. 2,000 m, 14 Feb. 1989, *van der Werff & Palacios 10575* (holotype, MO; isotypes, AAU, QAME, QCE, NY, K, US). Figures 2A, 4C–F.

Ab congeneribus foliis magnis, inflorescentiis tomentellis et floribus pedicellisque glabris differt.

Tree, 25 m, with divided buttresses. Twigs angular, solid, when very young yellow-brown tomentellous, the indument becoming gray and sparser on old twigs. Terminal bud densely yellow-brown pubescent. Leaves alternate, chartaceous, 15–25 × 8–15 cm, broadly elliptic or elliptic-oblong,the tip shortly acuminate, the acumen ca. 1 cm long, the base cuneate or narrowly acute, midrib and lateral veins impressed on upper surface, prominently raised on lower surface, the tertiary venation less raised; lateral veins 3–5 on each side, the basal pair much more strongly developed than the upper ones, thus the leaves subtripliveined, the second pair of lateral veins near or above the middle of the lamina; upper surface glabrous with the exception of some pubescence on midrib and basal lateral veins, lower surface sparsely (occasionally densely) appressed pubescent with the hairs not all oriented in the same direction, barbellate in the axils of the lateral veins. Petioles 2–3 cm long, canaliculate, with similar indument as twigs. Inflorescences single or a few together on short, leafless spurs, 4–14 cm long, paniculate, with the ultimate divisions cymose or sometimes appearing racemose through loss of the lateral flowers of a cyme, densely yellow-brown tomentellous, especially along the main axis; bracts frequently present, tomentellous-pilose on outside, glabrous inside, 1–3 mm long, ovate to (very) narrowly ovate; pedicels and flowers glabrous and contrasting markedly with the pubescent inflorescence. Pedicels terete, to 5 mm long, the lateral flowers of a cyme often with shorter pedicels. Flowers green, smelling of urine. Tepals 6, equal, erect at anthesis, ovate, 3–3.5 mm long at anthesis, glabrous outside, the 3 inner ones pubescent inside, especially toward the base. Stamens 9, all 4-celled, the outer 6 with the introrse cells arranged in 2 horizontal rows; the anther ca. 1 mm long, about as long as the pubescent filament; inner 3 stamens with narrow anthers, the cells lateral-extrorse, filaments with 2 large glands near the base and slightly longer than the anthers; staminodia 3, 1.5 mm long, the cordate tip ca. 0.8 mm long, filament pubescent; ovary glabrous, globose, style slender, ca. 1.5 mm long. Receptacle pubescent inside. Fruit unknown.

Cinnamomum palaciosii, known only from the type collection, belongs to *Phoebe* subg. *Phoebe* sensu Mez. Within this subgenus, it keys to *Cinnamomum salicifolium* (Nees) Kostermans, a poorly known Mexican species with much smaller leaves and smaller flowers. The new species can be readily recognized by its large, tripliveined leaves with an angustate or cuneate base, and the rather large, glabrous flowers contrasting with the tomentellous inflorescence.

It is a pleasure to name this species after Ing. Walter Palacios, who accompanied me on several field trips in Ecuador and who has collected several undescribed species of Lauraceae.

Endlicheria citriodora van der Werff, sp. nov. TYPE: Peru. Loreto: Maynas, Jenaro Herrera, roadside near the arboretum, 7 Aug. 1988 (fl), *van der Werff, Vásquez & Jaramillo 9991*, ♂ (holotype, MO; isotypes, AMAZ, HBG). Figures 2C, 4A, B.

A congeneribus foliis subtus glaucis, indumento ramulorum brunneo et ramulis citriodoris diversa est.

Dioecious tree, to 25 m tall. Twigs longitudinally ridged, roundish, densely brown-tomentellous with the odor of lemon and anise, the lemon scent dominating. Terminal bud brown-tomentellous. Leaves alternate, firmly chartaceous, 15–30 × 7–14 cm, elliptic, oblong or elliptic-ovate, the base obtuse, tip sharply acute to acuminate, the upper surface glabrous except for the tomentellous midvein, the lower surface glaucous and with varying amounts of small, appressed hairs, these never obscuring the surface; lateral veins 7–10 on each side, arching upward near the margin but not becoming loop-connected, immersed on the upper surface, raised on the lower surface, the midvein prominently raised below, tertiary venation faintly visible on both surfaces. Petioles 2–3.5 cm long, with similar indument as twigs, the adaxial side flat, the abaxial side rounded. Inflorescences reddish, in axils of regular leaves or cataphylls, 10–15 cm long, brown-tomentellous, 2–3 times branched, the ultimate branching cymose; in staminate plants the ultimate cymes usually sessile, the flowers thus in dense groups of 6–7 (rarely 9 or 13) flowers. Pedicels 1.5–2.5 mm long and flowers densely, minutely pubescent, the indument covering the surface entirely. Receptacle deep, ca. 0.7 mm long, slightly constricted near the tip, densely pubescent inside. Tepals 6, equal, spreading at anthesis, the tips bent inward, ca. 0.7 mm long, ovate-elliptic, with some

hairs on the inner surface. Male flowers: tepals reddish and stamens yellow, at anthesis the tepals spreading and the stamens fully exposed. Stamens 9, all 2-celled, the outer 6 ca. 0.5 mm long, almost sessile, the filament narrower than the anther, the cells large, the connective extending beyond the cells, filament with some hairs at the base; inner 3 stamens with extrorse cells, 0.7 mm long, the pubescent filament about as long as and wider than the anther; no glands seen on the filaments. Pistillode threadlike, glabrous, without a stigma, not surpassing the stamens. Female flowers: tepals at anthesis erect, the tips slightly incurved. Staminodes 0.3–0.5 mm long, the filaments broad, pubescent, anthers 2-celled, the cells opening. Staminodes surpassed by the style and more or less hidden under the stigma. Pistil 1.2–1.5 mm long, glabrous, ovary about as long and wide as the style, stigma large, peltate. Cupule shallowly cupshaped, red in vivo, smooth, 1.1 × 1.9 cm; in sicco black, this contrasting sharply with the tan-pubescent pedicel. Fruit ellipsoid, ca. 2.5 × 1.5 cm.

Paratypes. PERU. LORETO: Requena, Jenaro Herrera, *A. Castillo 13*, ♂ (fl) (MO), tree 4-478, *A., Castillo 34*, ♂ (fl) (MO), *Vásquez & Jaramillo 9593*, ♂ (fl) (MO, AMAZ); Maynas, Puerto Almendras *van der Werff et al. 9776* (st) (MO, AMAZ); Maynas, Mishana, *Gentry et al. 25983* (st) (MO) *Gentry et al. 39301* (fr) (MO), *van der Werff et al. 10187*, ♀ (fl) (MO, AMAZ); Maynas, Alpahuayo, field station of IIAP, *van der Werff et al. 10242*, ♂ (fl) (MO, AMAZ).

Flowers: August–September; fruits January. Common names: Limón-moena, Anis moena.

Endlicheria citriodora has been collected in the vicinity of Iquitos and Jenaro Herrera in Amazonian Peru. It is restricted to a forest type locally called "varillal," a ca. 25–30-m-tall, closed forest on a substrate of predominantly white sand with a small amount of clay. The glaucous lower leaf surface and the lemon scent are very good field characters; the scent is less pronounced in dried material, and specimens preserved in alcohol lose the glaucous cast. The two Castillo collections have retained the striking glaucous lower leaf surfaces.

The deep floral tube, constricted near the apex, resembles the shape of *Aniba* flowers. However, the unisexual flowers, anthers with large locelli and the smooth, fleshy cupule are characteristic of *Endlicheria*. This genus was last revised by Kostermans (1937) and is in need of an updated treatment. The closest relatives of *E. citriodora* are in the group of species with a deep receptacle and spreading tepals (*E. klugii* O. C. Schmidt, *E. browniana* Mez, *E. pyriformis* (Nees) Mez, *E. metallica* Kostermans, among others). The glaucous lower leaf surface, the indument of twigs and inflorescence and the lemon odor make identification easy, however.

An unusual character of the staminate inflorescences is the frequent suppression of the peduncles of the ultimate cymes. Thus, the flowers appear in pseudo-umbellate clusters, mostly consisting of six flowers (two cymes along an axis), or seven flowers (a terminal cyme with the two lateral divisions again cymosely branched). Occasionally, when the ultimate part of the main axis also becomes suppressed, the pseudo-umbels may consist of nine (one terminal and two lateral cymes condensed) or 13 (two lateral and a branched terminal cyme) flowers. Frequently, the number of flowers is smaller, because the central flowers of each cyme develop faster than the laterals and fall off before the laterals.

Ocotea alata van der Werff, sp. nov. TYPE: Peru. Loreto: Maynas, Mishana, Río Nanay halfway between Iquitos and Santa María de Nanay, upland forest on white sand, 12–13 Jan. 1983, ♀ (fl), *Gentry et al. 39447* (holotype, MO). Figure 2D.

Ab *Ocotea glomerata* et *O. magnifica* ramulis alatis et foliis basi rotundatis vel subcordatis recedit.

Dioecious tree to 20 m tall, but mostly less than 10 m. Twigs winged, the wings to 5 mm broad, young twigs densely tomentellous, glabrescent with age. Terminal bud densely tomentellous. Leaves alternate, chartaceous, 35–65 × 10–20 cm, (narrowly) obovate or elliptic, the base abruptly rounded to subcordate, the tip acute to acuminate, the upper surface glabrous, the lower surface with short, erect hairs ca. 0.2 mm long, the pubescence sparser and shorter on old leaves, the surface always visible; venation immersed on upper surface, midvein prominently raised on lower surface, the lateral veins (15–20 on each side) raised and tertiary venation slightly raised; lateral veins arching upward near the margin and becoming weakly loop-connected in the upper half of the lamina. Petioles 1–1.5 cm long, to 6 mm thick, canaliculate, with the same indument as twigs. Inflorescences in axils of leaves or cataphylls, 15–25 cm long, densely tomentellous, the lateral branches once or twice cymosely branched, many-flowered. Flowers sessile or nearly so, white, the tepals erect at anthesis. Tepals 6, equal, 1.5–2.0 mm long, densely appressed pubescent outside, sparsely pubescent inside, broadly ovate-elliptic. Male flowers: stamens 9, all 4-celled, glabrous, the outer 6 with introrse

cells, ca. 1 mm long, the filaments distinct, 0.4 mm long; inner 3 stamens fused, ca. 1 mm long, the cells extrorse; glands small, globose, attached at the base of the inner stamens; pistillode linear, enclosed by the inner stamens, with a small stigma, glabrous, the receptacle pubescent inside. Female flowers: staminodes 9, traces of anther cells visible but locelli not opening, inner 3 staminodes free; stigma platelike, raised above the staminodes, ovary globose, glabrous, enclosed in the glabrous receptacle. Tepals initially persisting in the fruiting stage, but finally deciduous. Immature fruit enclosed in receptacle, mature fruit ovoid, ca. 15 × 9 mm, largely exserted, the cupule deeply cup-shaped.

Distribution: Amazonian Peru, from Jenaro Herrera downstream to the Brazilian border.

Paratypes. PERU. LORETO: Prov. Requena, Jenaro Herrera, *Gentry et al. 21199*, ♂ (fl) (MO); *Spichiger & Encarnación 1167*, tree 6/125, ♂ (fl) (MO); *Vásquez & Jaramillo 232*, ♂ (fl) (MO); *van der Werff et al. 10089*, (st) (MO); collector unknown, tree 6/125, ♂ (fl) (MO); Prov. Loreto, Nauta, *Vásquez & Jaramillo 5059*, ♂ (fl) (MO); *Revilla 925* (young fr) (MO), *1640*, ♂ (fl) (MO); *Rimachi 3745* (fr) (MO); *Vásquez & Jaramillo 4483*, ♂ (fl) (MO), *8697*, (young fr) (MO), *8918*, (fr) (MO); Prov. Maynas, border post on Río Javeri, *Gentry & Revilla 20897* (fr) (MO).

Flowers year round (January, April, June, July, October, November, December); fruits collected in March, July, and November.

Ocotea alata belongs to the *O. guianensis* group of Rohwer (1986) because of its nearly sessile flowers, the fused stamens of whorl III, the persistent tepals of the young fruit, and the cupule shape. Within this group, it is most closely related to *O. glomerata* (Nees) Mez s.l., the only species with erect pubescence on the lower leaf surface. Part of *O. glomerata* s.l. is *O. magnifica* O.C. Schmidt (isotype, NY). This segregate has larger leaves with an inrolled base and a typical indument on the lower leaf surface (a dense, tomentellous pubescence and longer erect hairs), and is only known to me from the type collected at the middle Ucuyali. Two recent collections from the Tingo María area have the pubescence characters of *O. magnifica*, but resemble *O. glomerata* in leaf size and absence of an inrolled base. More collections are needed to determine the status of *O. magnifica*. *Ocotea alata* resembles *O. magnifica* in leaf size, but can be easily recognized by its winged stems and rounded leaf base. In the past, I have identified all cited specimens as *O. magnifica* and duplicates have been distributed under that name. Spichiger et al. (1989) also used the name *O. magnifica* for specimens from Jenaro Herrera; their illustration does not show the abruptly rounded leaf base, although they correctly describe this character. *Ocotea alata* occurs in varillal (see previous species).

Ocotea infrafoveolata van der Werff, sp. nov.
TYPE: Ecuador. Zamora–Chinchipe: at the pass of the Loja–Zamora road, wet scrub, elev. 2,900 m, 12 Feb. 1985, *Harling & Andersson 21968* (holotype, GB; isotype, MO). Figure 5.

Arbor parva, ramulis crassis, juvenalibus ferrugineo-tomentosis, vetustioribus glabris; foliis ellipticis, subtus ferrugineo-tomentosis, valde foveolatis; inflorescentiis axillaribus, paniculatis; floribus hermaphroditis, ca. 1 cm diametro; staminibus 9, 4-locellatis; staminodiis nullis, cupula parva.

Shrub or small tree, 6(–10) m tall. Twigs angular, ferruginous tomentose when young, becoming glabrous, often with conspicuous scars of fallen leaves. Leaves alternate, 6–15 × 2.5–6 cm, strongly coriaceous, elliptic to elliptic-oblong, the tip acute, the base gradually narrowed, at the very base revolute and decurrent on the petiole; the upper surface of very young leaves tomentose, this tomentum soon disappearing and the surface shiny and glabrous except for traces of tomentum on the main veins and the margin; lower surface with a dense, ferruginous tomentum, the midvein, secondary and tertiary veins with a lanate ferruginous pubescence, the surface between veins covered with a shorter, lighter-colored tomentose pubescence, or rarely the tomentum absent, both kinds of pubescence thinner and lighter colored with age; lateral veins 10–15 pairs, midvein and lateral veins immersed on upper surfaces, but, together with tertiary venation, prominently raised on the lower surface, which is strongly pitted by the raised reticulation; margin of the leaves revolute, more strongly so toward the base of the leaves. Petioles broad, ca. 5 mm wide, and to 1 cm long, but mostly poorly defined because of the decurrent laminae; pubescence on young petioles a ferruginous tomentum, this wearing off with age. Inflorescences axillary, paniculate, 10–16 cm long, branching in the upper half, the peduncle to 10 cm long; bracts supporting the basal branchlets of large inflorescences occasionally leaflike and persisting; inflorescence ferruginous tomentose near base, becoming ferruginous lanate in the distal part. Flowers hermaphrodite, greenish yellow, sessile or nearly so, subtended by a narrowly ovate, ferruginous tomentose bract, to 5 mm long. Tepals 6, equal, spreading ovate, 4 mm long, 3 mm wide, ferru-

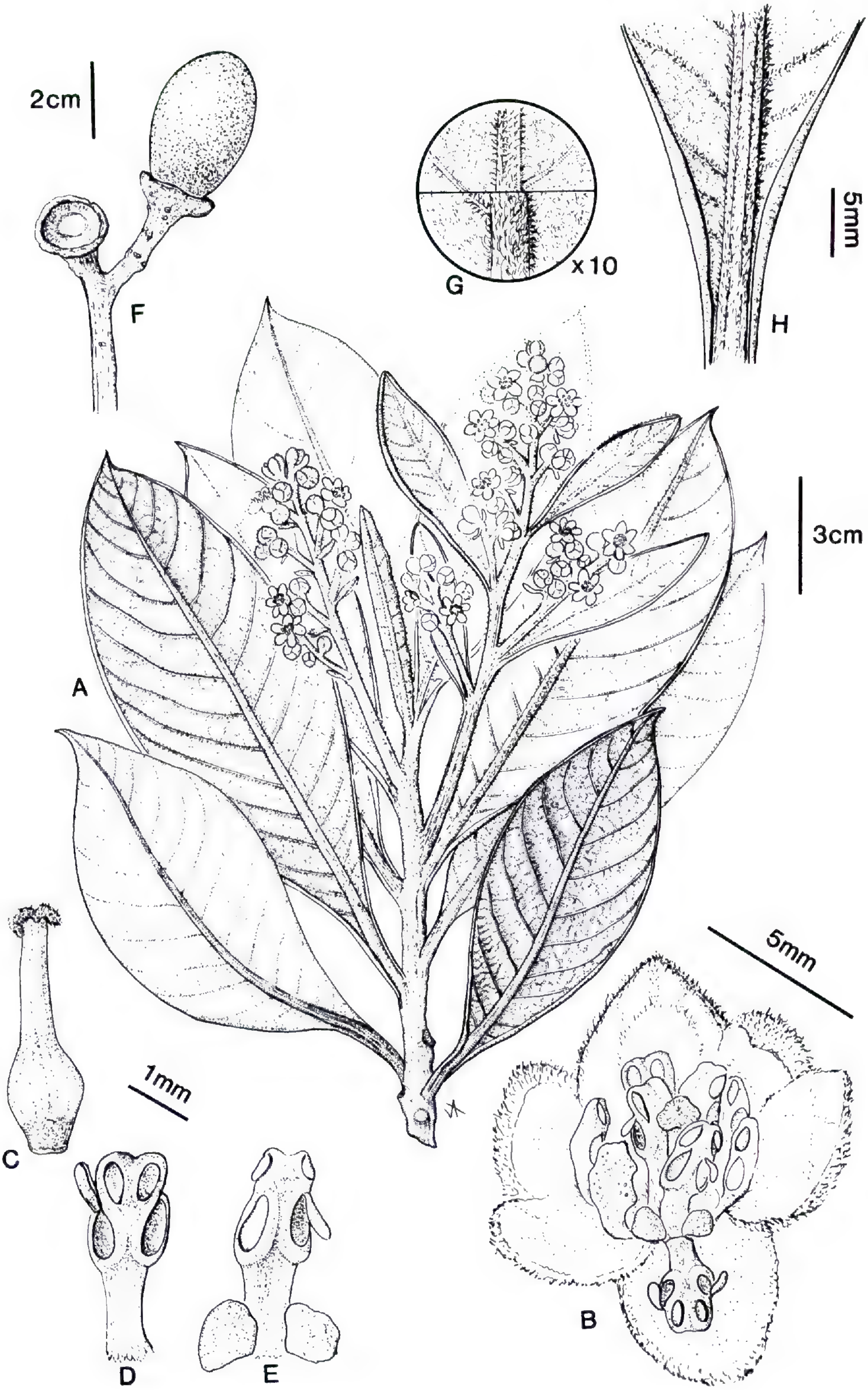

FIGURE 5. *Ocotea infrafoveolata.*—A. Habit.—B. Flower.—C. Pistil.—D. Stamen of whorl I/II, ventral view.—E. Stamen whorl III, dorsal view.—F. Cupule and fruit.—G. Detail of pubescence along midrib on lower leaf surface (lower half) and upper leaf surface (upper half).—H. Leaf base.

ginous tomentose outside, the pubescence more appressed on the inner face of the tepals; fertile stamens 9, all 4-celled, the outer 6 with introrse cells, the filaments glabrous or with few hairs, ca. 0.5 mm wide and 1 mm long, the anthers glabrous, ca. 0.8 mm wide and 1.2 mm long; inner 3 stamens with extrorse cells, the filaments with 2 glands near the base, filaments and anthers each ca. 1 mm long; staminodia lacking; ovary glabrous, enclosed in the cupshaped, pubescent floral tube, globose, ca. 1 mm diam.; style ca. 2 mm long, the stigma platelike, ca. 0.7 mm diam. Infructescence woody, glabrous, the cupule a shallow, small cup, ca. 1.5 cm wide and 0.7 cm tall (outside) with few, rather large lenticels. Fruit a 1-seeded berry, broadly ellipsoid, to 3 cm long and 2.5 cm wide when dry; young cupule with weakly lobed margin, margin becoming straight at maturity.

Paratypes. COLOMBIA. DEPTO. CAUCA: *Cuadros 359* (MO), *Cuatrecasas 18942* (MO, F). DEPTO. NARIÑO: *Soejarto 1999* (F). DEPTO. DEL VALLE: *Cuatrecasas 17910* (F), *Cuatrecasas 20418* (F), *Cuatrecasas 20588* (F), *Cuatrecasas 21906* (F, US), *Cuatrecasas 21922* (F, U), *Devia 649.* ECUADOR. PROVINCE CARCHI: *Balslev et al. 2620* (AAU, NY), *Tipaz 10* (MO, QAME), *Tipaz 85* (MO, QAME), *Tipaz 87* (MO, QAME). PROVINCE NAPO: *Holm-Nielsen et al. 29858* (AAU), *Jaramillo 7686* (GB). PROVINCE AZUAY: *Camp E-4808* (MO, NY), *Harling & Andersson 21177* (GB), *Jaramillo 7149* (GB), *Knight 218* (WIS), *Steyermark 53424, 53425* (F). PROVINCE LOJA: *van der Werff & Palacios 9426* (AAU, HBG, MO, QAME). PROVINCE UNKNOWN: *Espinosa 1087* (F, NY).

Flowers and fruits year-round.

Ocotea infrafoveolata is a high-elevation (between 2,600 and 3,400 m) shrub or small tree, only known from southern Colombia and adjacent northern Ecuador and south of Cuenca in Ecuador, with one collection in central Ecuador. Its affinities in *Ocotea*, a largely neotropical genus of probably more than 300 species, are not clear. The shape of the inflorescence, the cupule, leaf shape, and decurrent leaf bases suggest an affinity to *O. calophylla* Mez, *O. sericea* HBK, and *O. micans* Mez, all densely pubescent, high-elevation species of northern South America and Costa Rica. However, none of these species have a foveolate lower leaf surface and all have unisexual flowers. Some collections of *O. infrafoveolata* have slightly smaller flowers than others, but locelli of both smaller and larger flowers contain pollen, even on specimens with old fruits. Because the unisexual character of *O. calophylla* and *O. sericea* is quite obvious, it is unlikely that the smaller and large flowers of *O. infrafoveolata* represent different sexes. Another difference is the absence of vernation lines on the leaves of *O. infrafoveolata*, while these are conspicuous on the leaves of *O. calophylla* and related species.

In spite of these differences, *O. infrafoveolata* seems to be related to the group of *O. calophylla*. There are other species of Lauraceae restricted to high elevations in the Andes and with a similar pubescence, but these species (in *Ocotea* and *Persea*) differ clearly in floral and cupule characters, and the ferruginous pubescence is more likely an adaptation to cold, wet habitats than an indication of taxonomic relationship.

Ocotea rotundata van der Werff, sp. nov. TYPE: Ecuador. Prov. Loja: Parque Nacional Podocarpus, along road from Yangana to radio tower on Cerro Toledo, cloud forest, 2,900 m, 29 Apr. 1987, *van der Werff & Palacios 9192* (holotype, MO; isotypes, AAU, HBG, QAME). Figures 6, 3G–J.

Ocoteae arnottianae similis, sed foliis rotundatis, petiolis brevioribus et pubescentia longiore differt.

Shrub or small tree, to 10 m tall. Twigs slightly angular and rufous tomentose when young, becoming terete and glabrous with age. Terminal bud ca. 9 mm long, rufous tomentose. Leaves alternate, 5–8 × 4.5–6 cm, broadly elliptic, the smallest leaves often roundish, coriaceous, the base rounded, the tip rounded or with a very short acumen, the upper surface glabrous (young leaves with some rufous pubescence along costa and veins, but this wearing off very quickly) and with costa and veins immersed, the lower surface rufous tomentose, color of the tomentum fading on old leaves and the tomentum wearing off, but leaves very rarely becoming glabrous, costa and veins elevated on lower surface, but tertiary venation not visible; margin plane, not thickened; veins 4–6 pairs, the lower 2 or 3 close together near the base of the leaf. Petioles 3–6 mm long, to 4 mm thick, with similar type and density of pubescence as the twigs. Inflorescences axillary, 6–12 cm long, rufous tomentose, paniculate or, when small, racemose, the flowers usually arranged in cymes. Flowers perfect, pale yellow or creamy, the floral tube deep and gradually narrowed in the very short pedicel. Pedicels, floral tubes, and the outside of the tepals ferruginous tomentose (inner tepals with glabrous margin and tip). Tepals 6, ovate, ca. 3 mm long, the inner surface with some papillose pubescence near the apex, this best visible in young flowers, otherwise glabrous. Stamens 9, all 4-celled (but many flowers with 1 or 2 cells apparently sterile; the position of the sterile cells variable), the cells arranged in 2 horizontal rows; filaments of the outer stamens ca.

FIGURE 6. *Ocotea rotundata.*

0.8 mm long, dorsally with a narrow row of hairs; anthers of the outer stamens curved inward, their cells introrse; inner stamens erect, ca. 1.6 mm long, the pubescent filament as long as the anther, glands large, attached near the base of the filament; upper pair of anther cells lateral, the lower pair extrorse; staminodia ca. 1 mm long, the lower part pubescent, the tip glabrous and swollen. Pistil ca. 2.5 mm long, glabrous; ovary enclosed in the deep floral tube, floral tube densely pubescent inside. Fruit ellipsoid, 2 × 1.5 cm, cupule funnelshaped, with a weakly developed double margin.

Paratypes ECUADOR. PROVINCE LOJA: Parque Nacional Podocarpus, *Molau & Eriksen 3217* (GB), *Larsen & Dall 229* (GB), *Stein & D'Alessandro 2718* (MO), *van der Werff & Palacios 9189, 9195, 9283, 9285, and 9321* (all MO, HBG, QAME).

Ocotea rotundata is known only from the Parque Nacional Podocarpus, to the south of Loja, at elevations of ca. 3,000 m. It only grows in wet habitats; it has not been collected on the drier slopes to the north and west of Loja, such as Cerro Villonaco. The new species belongs to the *Ocotea aciphylla* (Nees) Mez group, as circumscribed by Rohwer (1986). Characteristics for this group are hermaphroditic flowers, a deep floral tube (and large cupule in fruit), rather large staminodia, and basal lateral veins that are close together. Although this group includes mostly lowland species, several Andean species (*O. arnottiana* (Nees) van der Werff, *O. heterochroma* Mez & Sodiro, *O. jelskii* Mez, and *O. stuebelii* Mez) belong here as well. These species, which are not well known, differ from *O. rotundata* in having narrower leaves with acute tips and bases and longer petioles, as well as in details of the pubescence. In leaf shape, *O. rotundata* is very similar to *O. julianii* van der Werff (*Phoebe steyermarkii* Allen; van der Werff, 1989). The latter is restricted to the summit areas of Chimantá-tepui, Edo. Bolívar, Venezuela, and differs in its shorter, often darker tomentum on the

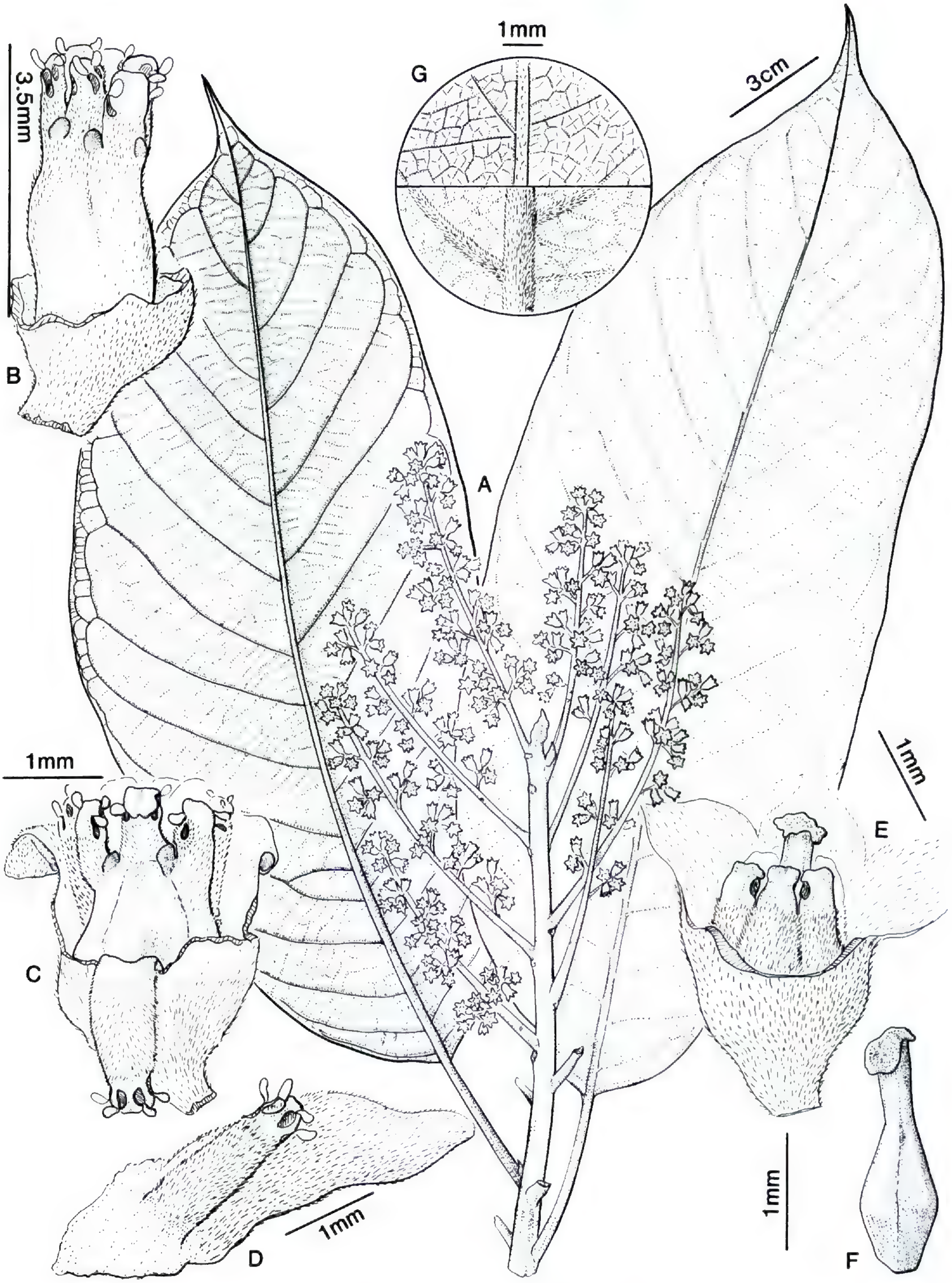

FIGURE 7. *Rhodostemonodaphne synandra*.—A. Habit.—B. Staminate flower, tepals and stamens of whorl I removed.—C. Staminate flower, showing free stamen of whorl I and partially fused stamens of whorls II and III.—D. Tepal with stamen of whorl I.—E. Pistillate flower, some tepals and stamens of whorl I removed.—F. Pistil.—G. Detail of pubescence and venation on lower leaf surface (lower half) and upper leaf surface (upper half).

leaves, shorter tomentum on the twigs, a much larger cupule and fruit, and its distribution.

Rhodostemonodaphne synandra van der Werff, sp. nov. TYPE: Ecuador. Napo: Estación Biológica Jatun Sacha, 8 km downstream from Puerto Misahualli, tree, 30 m, ♂ flowers green, *Neill & Palacios 7129* (holotype, MO; isotypes, QAME, HBG). Figure 7.

Ab *R. kunthiana* foliis oblongis, pubescentia cinnamomea, floribus glomeratis, filamentis staminum serierum II and III ⅔ connatis, et glandulis minoribus late differt.

Dioecious tree, to 30 m. Twigs hollow, slightly angled to round, densely yellow-brown tomentellous when young, the indumentum diminishing with age. Terminal bud densely tomentellous. Leaves alternate, elliptic or oblong, 20–30 × 7–11 cm, stiffly chartaceous, the base acute or obtuse, the apex acuminate; upper surface glabrous (except some pubescence on the midrib), often shiny, midrib and lateral veins immersed, but tertiary venation raised; lower surface with raised midrib, lateral veins and tertiary venation, the entire venation system laxly tomentellous; lateral veins 10–15 pairs. Petioles 2–3 cm long, brown-tomentellous, canaliculate. Staminate inflorescences axillary, to 10 cm long, yellow-brown tomentellous; the lower flowers of the inflorescence clustered near the tips of lateral axes, these axes becoming shorter toward the tips of the inflorescence; pistillate inflorescences to 7 cm long, unbranched, the flowers clustered along the main axis. Flowers gray-tomentellous, sessile or nearly so, campanulate, 3 (dry) to 5 (after boiling) mm long. Staminate flowers: tepals 6, equal, spreading to reflexed at anthesis, tomentellous outside, sparsely pubescent and slightly papillate inside, ca. 2 × 1.2 mm. Stamens 9, all 4-celled; outer 3 stamens attached near the base of the floral tube, ca. 3 mm long, the pubescent filament wider than the glabrous anther, the upper cells introrse, the lower lateral; stamens of whorl II and whorl III ca. 3 mm long, their filaments fused for the lower 2 mm and free for the upper 1 mm, forming a central column; anthers of whorl II with introrse cells, of whorl III with extrorse cells; stamens of whorl III with 2 glands attached at the base of the free part of the filament; staminodia (whorl IV) and pistillode not seen. Floral tube pubescent inside. Pistillate flowers: staminodia of whorl I ca. 1.5 mm long, free, the thick, fleshy filament pubescent, the tip glabrous, cells rudimentary, introrse; filaments of whorls II and III partly connate, only upper part free; glands of whorl III attached at the base of the free part of the stamens, glabrous, small; ovary ellipsoid, ca. 2 mm long, glabrous; style distinct, ca. 1.5 mm long; floral tube glabrous inside. Fruits unknown.

Paratype PERU. HUANUCO: Fundo Sinchona, km 209 carretera Huanuco–Pucallpo, 1,200 m, *Hodge & Lescano 1*, ♀ (fl) (F); same locality, *Lescano 2* ♀ (fl) (MAD).

Rhodostemonodaphne synandra is only known from the three cited collections. The two Peruvian collections carry exactly the same label information, were both collected on 9 October, and are both pistillate; it is probable that they are the same collection and that the label erroneously states that one specimen (MAD) was collected in 1945 and the other (F) specimen in 1944.

Vegetatively, *Rhodostemonodaphne synandra* is quite similar to the widespread *R. kunthiana* (Mez) Rohwer. *Rhodostemonodaphne synandra* differs in its yellow-brown pubescence (ferruginous brown in *R. kunthiana*) and its narrower, more oblong leaves. The inflorescence of *R. synandra* is smaller, with clustered, nearly sessile flowers. The flowers themselves are highly diagnostic. They are larger than in *R. kunthiana*, and the stamens are attached near the bottom of the floral tube, not near the margin, as in *R. kunthiana*. The filaments are, for the genus, very long, but even more remarkable is that the filaments of the stamens of whorls II and III are fused for ⅔ of their length. Usually, when there are differences between the staminal whorls in Lauraceae flowers, whorls I and II are similar and differ from whorl III, for instance in *Kubitzkia*, where the filaments of whorl III are fused, but those whorls I and II are free. Thus, the situation in *R. synandra*, where whorl I is separate from the fused whorls II and III, is highly unusual. An additional difference between *R. synandra* and *R. kunthiana* is that *R. kunthiana* has large, staminal glands which are visible between the outer stamens at anthesis, whereas in *R. synandra* the glands are small and only visible in dissected flowers. Meissner (1864) coined the name *Synandrodaphne* because the very bases of the stamens were fused into a ring like structure. I use the epithet *synandra* for a different reason, namely the fusion of the filaments of the stamens of whorls II and III.

Rhodostemonodaphne is a small neotropical genus of about ten species, recently named by Rohwer & Kubitzki (1985), who raised *Nectandra* subg. *Synandrodaphne* to generic level. Because *Synandrodaphne* Gilg is conserved over *Synandrodaphne* Meissner, they proposed the name *Rhodostemonodaphne*. With two exceptions (*R. grandis* (Mez) Rohwer and *R. kunthiana* (Nees)

Rohwer), the species placed in *Rhodostemonodaphne* by Rohwer (1986) are very poorly known. *Rhodostemonodaphne* is characterized by the following combination of characters: flowers unisexual; anthers 4-celled, the cells arranged in an arc; filaments poorly (or not at all) differentiated from the anther; staminodia lacking; and pubescence usually dense. The exclusion of *Rhodostemonodaphne* from *Nectandra* strengthens the unity of *Nectandra* and seems fully justified.

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REVISIONARY STUDIES IN THE ERIOCAULACEAE OF VENEZUELA[1]

Nancy Hensold[2]

ABSTRACT

Preparation of the Eriocaulaceae treatment for Julian Steyermark's *Flora of the Venezuelan Guayana* has brought to light a new achene-bearing subgenus, *Paepalanthus* subg. *Monosperma*, as well as the following six new species and one variety: *Eriocaulon spongiola*, *Paepalanthus chimantensis*, *P. fasciculoides*, *Syngonanthus acephalus*, *S. duidae* var. *humilis*, *S. fenestratus*, and *S. setifolius*. In addition, 14 new names or combinations are made, and some instances of synonymy are discussed.

The Guayana Highland, particularly in Venezuela, is one of the two major centers of distribution for the Eriocaulaceae in the New World, the second area being the Brazilian Central Plateau. Of the approximately 100 species of Eriocaulaceae occurring in Venezuela, about 85 occur in Guayana, 38 of which are endemic there. In preparation of the Eriocaulaceae treatment for the *Flora of the Venezuelan Guayana* (Julian Steyermark, editor), several new taxa of the region have come to light, and many revisionary changes have been found necessary. Of special interest are: *Eriocaulon spongiola*, a species with floating ribbonlike peduncles and spongy hygroscopic involucral bracts; a dimerous species of *Syngonanthus*, with exceptionally reduced inflorescences lacking peduncles and involucres; and a new subgenus of *Paepalanthus* producing single-seeded indehiscent fruits, the only known departure in the family from 3-locular capsules.

ERIOCAULON

Eriocaulon spongiola Hensold, sp. nov. TYPE: Colombia. Vaupés: Rio Apaporis, Rio Piraparaná, Cano Teemeeña, between 0°15′S, 70°30′W and 0°25′N, 70°30′W, *Schultes & Cabrera 17314* (holotype, US; isotype, MO). Figures 1, 2.

Planta aquatica caulescens. Folia fasciaria, membranacea, valde fenestrata, fluitantia, usque 30 cm longa et 5–7 mm lata. Pedunculi basin versus filiformes apicem versus fasciarii, fenestrati, 2–3 mm lati, folia simulantes. Capitula 5–6 mm lata. Bracteae involucrales pallide brunneae, apicibus spongiosis hygroscopicis auctae. Flores trimeri; sepala libera vel in spatha connata; petala subaequalia; antherae albidae.

Plants aquatics in shallow streams, the base rooted, the stems, leaves, and peduncles submerged or floating. Roots relatively fine, ca. 0.5 mm diam. Stems up to 25–30 cm long, ca. 1–2.5 mm wide, glabrous. Leaves linear, ribbonlike, up to 30 cm or longer and 5–7 mm wide, membranous, glabrous, the tips often broken off, conspicuously fenestrate from base to apex, the longitudinal and transverse striations of about equal thickness. Inflorescence arrangement unknown (peduncles not attached to the stem in the available material). Peduncles 40–50 cm long, filiform at base, broadening and ribbonlike toward the apex, up to 2.5–4 mm wide, membranous, glabrous, fenestrate like the leaves, not evidently costate. Capitula 5–6 mm diam., hemispheric to ovoid, with an elongate receptacle. Involucral bracts in only 1–2 series, orbicular or somewhat tapered toward the irregularly rounded apex, ca. 1.5–2.2 mm long and nearly as wide, spongy, pale brownish, glabrous. Floral bracts similar in size and color to the involucral bracts, the base broad, carinate, and membranous, held perpendicular to the elongate receptacle and cupping the flowers, the apex abruptly differentiated from the base, broadly rounded to truncate or

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FIGURE 1. *Eriocaulon spongiola* Hensold (*Schultes & Cabrera 17314* US).—A. Habit.—B. Leaf.—C. Inflorescence.—D. Involucral bract.

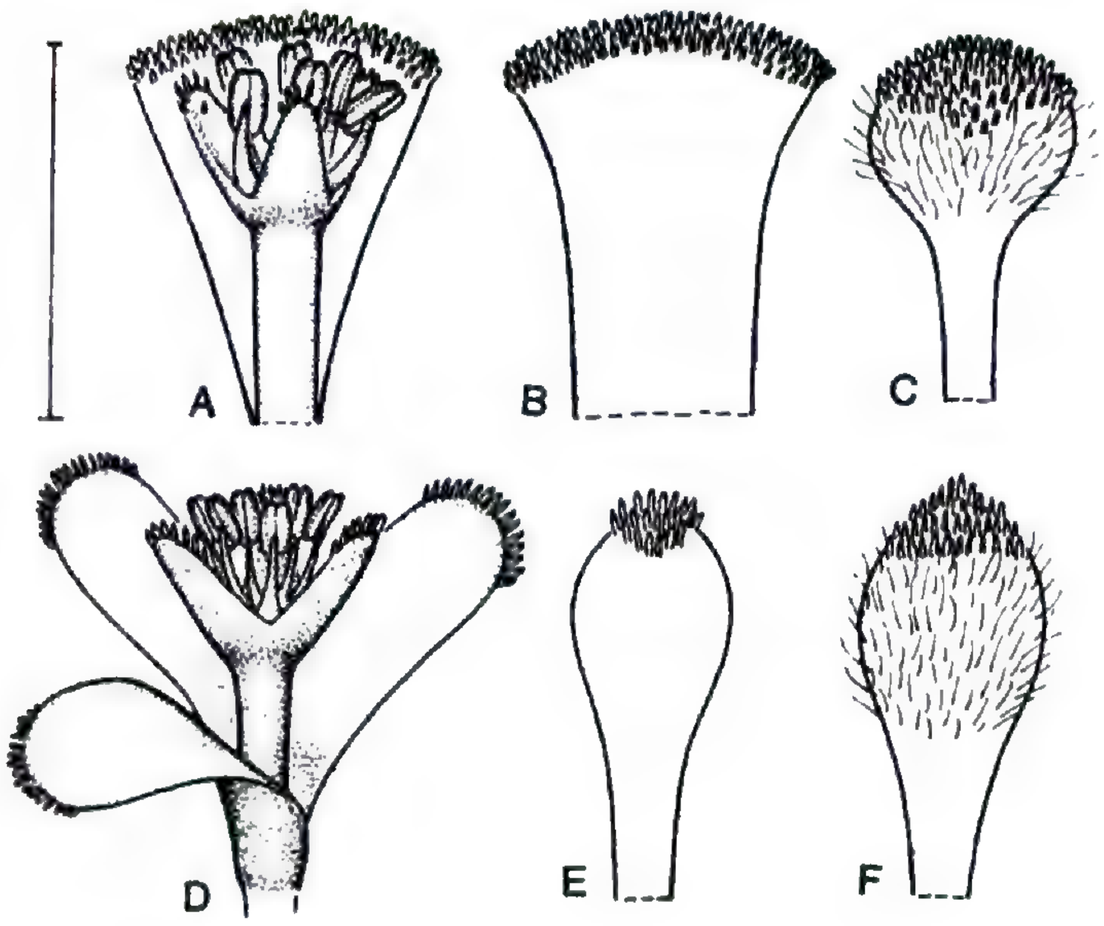

FIGURE 2. *Eriocaulon spongiola* Hensold. A–C. *Berry 746* (VEN).—A. Staminate flower, the calyx fused into a truncate spathe. B, C. Pistillate flower.—B. Calyx.—C. Petal, adaxial view. D, E. *Schultes & Cabrera 17314* (US).—D. Staminate flower, the calyx only shallowly fused, regular. E, F. Pistillate flower.—E. Sepal, abaxial view.—F. Petal, adaxial view. Scale bar = 1.5 mm.

triangular-obtuse (progressively smaller distally), spongy, hygroscopic, expanding and folding upward against the surface of the capitulum to enclose the flowers when wet, pilose abaxially with white, clavate hairs in a transverse band below the apex. *Staminate flowers*. Sepals 3, free, oblong and rounded (Colombia) or completely fused into a cuneate, perfectly truncate adaxial spathe (Venezuela), in either case ca. 1.9–2.4 mm long, light brown, membranous, densely ciliate with white clavate hairs at the upper margin. Androphore ca. 1.3–2.0 mm long, ca. 0.25 mm diam. Petals free, equal or subequal, ca. 0.4 mm long, pilose at the upper margin and adaxially at the apex, glandular (Venezuela) or not (Colombia). Stamens with filaments about equaling the petals; anthers white, ca. 0.25 mm long. *Pistillate flowers*. Sepals 3, free, spatulate (Colombia) or completely fused into a spathe as in the staminate flowers (Venezuela), in either case ca. 1.5–1.6 mm long, the same color, texture, and pubescence as in the staminate flowers. Petals free, broadly spatulate, rounded, about equaling the sepals, tufted with white clavate hairs adaxially at apex, and also pubescent with curly brownish filamentous hairs adaxially below apex, glandular (Venezuela) or not (Colombia).

Additional specimen examined. VENEZUELA. AMAZONAS: in caño ca. 4 km S of Macuruco on road to Santa Bárbara del Orinoco, *Berry 746* (VEN) (inflorescences only).

This species had previously been mistaken for *E. spruceanum* Koern., which also may have floating, membranous, ribbonlike leaves, and which may occur in the same general area (though it is not known from Venezuelan Guayana). *Eriocaulon spongiola* is easily distinguished by its elongate stem, its very conspicuously fenestrate leaves, and particularly by its fenestrate, membranous peduncles and the spongy, hygroscopic apices of the floral bracts. *Eriocaulon spruceanum* also has fenestrate leaves, but these often must be held up to the light for the transverse striations to be clearly seen, and these tend to be finer and less conspicuous than the longitudinal striations. In addition, *E. spruceanum* almost always has firm, erect, conspicuously costate peduncles, which are never fenestrate.

Because floral morphology, particularly sepal form and fusion, seems to be a very plastic character in *Eriocaulon*, I have not recognized the Venezuelan material, with sepals fused into a cuneate spathe, as distinct from the Colombian material, with the sepals completely free.

PAEPALANTHUS

Paepalanthus subg. **Monosperma** Hensold, subg. nov. TYPE: *Paepalanthus squamuliferus* (Mold.)

Herba perennis caulescens vel rosulata rhizomatosa. Radices veteres saepe villosae. Flores pistillati: Sepala demum non nisi secus costam incrassata, in capitulo remanentia. Petala plerumque dense longiciliata, demum omnino incrassata cum fructu dispersa. Appendices styli plerumque nigricantes, non nisi apice papillosae, ramulos styli fere aequantes. Stigmata bifida. Ovarium semen unum efferens; fructus achenium.

Caulescent or rhizomatous rosulate perennial herbs. Roots firm, usually whitish, the epidermis even of older roots, often persistently villous on exposed aboveground portions. Leaves linear to ligulate or lanceolate, chartaceous to coriaceous, smooth above and striate below or the upper surface 1–3-sulcate, variously pubescent with filamentous hairs. Inflorescences solitary to numerous, the peduncle sheaths foliaceous with an acute apex. Capitula 4–16 mm diam., hemispheric to globose or fungiform. Involucral bracts mostly dark blackish brown, occasionally paler and then dull yellow-brown or copper-colored, ± ovate, the apex obtuse to acute, acuminate or apiculate, enclosing but never surpassing the head, glabrous to ciliate and abaxially sericeous. Receptacle pilose. Floral bracts oblanceolate to oblong or squarish, subequaling the flowers, dark brown, barbate abaxially at apex, the

trichomes linear-obtuse to clavate, granular within. Flowers 3-merous, unisexual, actinomorphic, short-pedicellate. *Staminate flowers*. Sepals free or briefly connate at base, oblanceolate to obovate, acute to rounded, dark brown, barbate abaxially. Corolla tubular, borne on an androphore, the androphore commonly stout and about equal to corolla tube in length, though sometimes much shorter, the tube rather narrowly infundibular, membranous, the lobes 3 and sharply triangular-acute or sometimes low, rounded, and irregular. Filaments free, the anthers exsert, white to brown. Pistillodes large, simulating appendages of gynoecium. *Pistillate flowers*. Sepals free, obovate to sometimes ovate or oblong, similar in color and pubescence to those of staminate flowers, the midrib area thickened and pale in fruit. Petals oblong to narrowly elliptic, lanceolate or oblanceolate, usually much narrower than sepals, blackish streaked, and usually densely pubescent with very long cilia, especially toward the base, rarely (*P. chimantensis*) subglabrous, thickening throughout and the tips recurving at maturity, dispersed with the fruit. Staminodes present at base of petals, small and scalelike and appressed against the ovary. Ovary dark blackish brown, producing a single seed, the two abortive locules represented by ridges in fruit; style frequently equaling or exceeding the style branches in length, never less than ½ the length of the style branches, robust, often somewhat swollen above, easily breaking just above the ovary, not dispersed with fruit; appendages large, stalked, fusiform to clavate, with the main body smooth and usually blackish, white-papillate only at the upper rim, about ⅔ to equal the length of the style branches; style branches shallowly bifid. Fruit an indehiscent single-seeded asymmetrically fusiform achene.

This subgenus comprises 23 species, all of which are endemic to the Guayana Shield of Venezuela, Amazonian Brazil, and Guyana. Most of the species are narrow endemics to the summits of one or few tepui formations. They are closely related to each other, distinguished by subtle, reticulately varying characters, and show some evidence of hybridization. This variation pattern is similar to that seen in certain eriocaul taxa of the Brazilian highlands (e.g., *Paepalanthus* subg. *Xeractis* and *Aphorocaulon*, and *Syngonanthus* sect. *Eulepis* in the Serra do Espinhaço of Minas Gerais). Although the topography of the Brazilian and Venezuelan highlands is very different, both areas represent seasonally wet high-altitude formations with thin, nutrient-poor soils.

Paepalanthus subg. *Monosperma* is the only subgenus of *Paepalanthus* to have undergone radiation on the tepui summits of Venezuela. Members of a few other alliances occasionally reach tepui summits (*P. dichotomus* Klotzsch ex Koern., *P. tortilis* (Bong.) Koern., and *P. formosus* Mold.), but the main distribution of these species and their allies is elsewhere.

This subgenus is best characterized by the apparently consistent production of single-seeded indehiscent fruits, in contrast to the capsular fruits produced by all other taxa known in the family. The achenes are dark-colored and thin-walled, not differing greatly in appearance from fruits of other *Paepalanthus* in which by chance only a single ovule has matured. At anthesis, the ovaries of subg. *Monosperma* are to my eye indistinguishable from those of other subgenera. It remains to be shown whether only one functional ovule is produced, or whether all three ovules are functional, with the development of more than one seed chemically inhibited. Thomas Stützel (pers. comm.) has pointed out that a consistent position of the fertile locule would provide evidence for the first possibility. Unfortunately, because the position of the "fertile locule" cannot be readily distinguished before seed set, and seed set occurs concomitant with abscission of floral parts from the axis, I have not been able to answer this question with the material at hand.

Whatever the mechanism, the character of single seed production appears to be constant throughout the subgenus. The regular abscission of the style from the apex of the ovary is further evidence that the character is genetically fixed. Such abscission is not observed in the capsular-fruited species, in which the seed, not the fruit, is the dispersal unit. Similarly, the sclerification of the petal bases in fruit also may be interpreted as evolutionarily correlated with indehiscent fruit production, because in capsular fruits this sclerification would impede seed dispersal.

Characters other than fruit type useful in distinguishing the subgenus are: (1) the villous indumentum on exposed portions of the root; (2) the sclerification of both perianth whorls of the pistillate flower in fruit (and not merely the sepals); (3) the relative weakness of sclerification of the sepals of pistillate flowers, and their failure to recoil hygroscopically upon drying, being left behind in the capitulum after fruit dispersal; (4) the extreme hairiness of the petals of the pistillate flowers in all but one species (*P. chimantensis*); (5) the very fleshy elongate style with long darkly pigmented nectaries papillate only at the upper rim (see flower of *P. chimantensis*, Fig. 4); and (6) the regular abscission of the style at fruiting.

It is not possible at this time to make a rigorous

comparison with other subgenera because the genus as a whole is poorly known, especially with respect to floral characters. The most complete description possible is provided in order to facilitate future comparisons with other as yet poorly known groups. Characters 1, 2, 5, and 6, above are to my knowledge rather exceptional in the genus. Characters 3 and 4 are useful in identification but are also found in other taxa.

The affinities of this subgenus are not yet clear, though it bears some similarity to a complex of capsular-fruited species native to the West Indies, represented by *Paepalanthus seslerioides* Griseb. and *P. retusus* Wright.

A list of accepted taxa and synonyms to be placed in the subgenus follows.

1. *P. apacarensis* Mold.
2. *P. auyantepuiensis* Mold.
3. *P. cardonae* Mold.
4. *P. chimantensis* Hensold, sp. nov.
5. *P. convexus* Gleason
6. *P. cumbricola* Mold.
7. *P. fraternus* N. E. Br.
8. *P. fulgidus* Mold.
   P. perplexans var. *steyermarkii* Mold. (syn.)
9. *P. gleasonii* Mold.
   P. robustus Gleason (syn.)
   P. convexus var. *strigosus* Mold. (syn.)
10. *P. holstii* Steyerm.
11. *P. kunhardtii* Mold.
12. *P. major* (Mold.) Hensold, comb. nov. (see below)
13. *P. parvicephalus* (Mold.) Hensold, comb. et stat. nov. (see below)

13a. *P. parvicephalus* var. *parvicephalus*

13b. *P. parvicephalus* var. *wurdackii* (Mold.) Hensold, comb. nov. (see below)

14. *P. phelpsae* Mold.
15. *P. roraimensis* Mold.
    Rondonanthus micropetalus Mold. (syn.)
16. *P. schomburgkii* Klotzsch ex Koern.
    P. perplexans Mold. (syn.)
    P. pendulus Mold. (syn.)
    P. macrocaulon var. *venamensis* Mold. (syn.)
17. *P. scopulorum* Mold.
    P. scopulorum var. *auyantepuiensis* Mold. (syn.)
18. *P. squamuliferus* Mold.
    P. fraternus var. *spathulatus* Mold. (syn.)
19. *P. stegolepoides* Mold.
    P. fraternus var. *chimantensis* Mold. (syn.)
20. *P. subcaulescens* N. E. Br.
21. *P. sulcatus* Hensold
    P. stegolepoides var. *acutalis* Mold. (syn.)
22. *P. turbinatus* (Gleason) Hensold, comb. nov. (see below)
23. *P. venustus* Mold.
    P. venustoides Mold. (syn.)

Paepalanthus chimantensis Hensold, sp. nov. TYPE: Venezuela. Bolívar: Apácara-tepui, Chimantá Massif, 2,200 m, 30 Jan.–1 Feb. 1983, *Huber & Steyermark 6971* (holotype, MO; isotype, VEN). Figures 3F, G, 4.

Herba perennis rosulata. Folia 3–4.5 cm longa, 3–8 mm lata, valde mucronata, subtus striata superne laevia nitida ubique glabra. Pedunculi ca. 13–30 cm longi basin versus glabri ad apicem sericeo-tomentosi. Capitula 6.5–9 mm lata. Bracteae involucrales griseo-brunneae angusteovatae plerumque breviter acuminatae, proximales distales subaequantes. Fructus achenium.

Rosulate rhizomatous perennials forming small clumps. Roots pale, fibrous. Leaves chartaceous, glabrous, often bluish green, 3–4.5 cm long, 3–8 mm wide at middle, tapered, usually rounded toward the apex, distinctly mucronate, the upper surface lustrous, especially shiny toward the margins, the lower surface striate. Inflorescences 1–6 per cohort, synchronous; peduncle sheaths equaling to exceeding leaves by up to 3.0 cm, glabrous, the apex acute to acuminate; peduncles ca. 13–30 cm long, 4–5-costate, lightly tomentose at least when young with mixed retrorse and antrorse hairs, usually glabrate toward base and more densely and persistently sericeo-tomentose distally. Heads 6.5–9 mm diam., hemispheric to subglobose at maturity; involucral bracts gray-brown, lustrous, ciliate in bud but early glabrate, lance-ovate, usually aristate or short-acuminate, the lower bracts slightly narrower than but usually as long as the upper, and usually with a slightly thickened reddish midrib. Floral bracts about equaling the flowers, obovate to linear-subspatulate, fuscous, subhyaline, ciliate at upper margin and tufted along midvein abaxially with opaque white clavate hairs. *Staminate flowers.* Pedicels ca. 1.0 mm long. Sepals 3, free, elliptic to narrowly obovate, acute, ca. 1.9–2.5 mm long, 0.7–1.2 mm wide, fuscous, pubescent as floral bracts; corolla tube borne on an androphore ca. 0.5–0.75 mm long, the tube itself 1.0–1.5 mm long, narrowly infundibular, the lobes 3, narrowly triangular, acute; anthers cream to brownish, strongly exsert; pistillodes 3, simulating gynoecial appendages and nearly the length of the tube. *Pistillate flowers.* Sepals 3, free, broadly obovate-elliptic, acute, carinate, ca. 2.8 mm long, 1.6 mm wide, fuscous at least toward the apex, pubescent as in the staminate flowers, the midvein area thickening and expanding at maturity toward

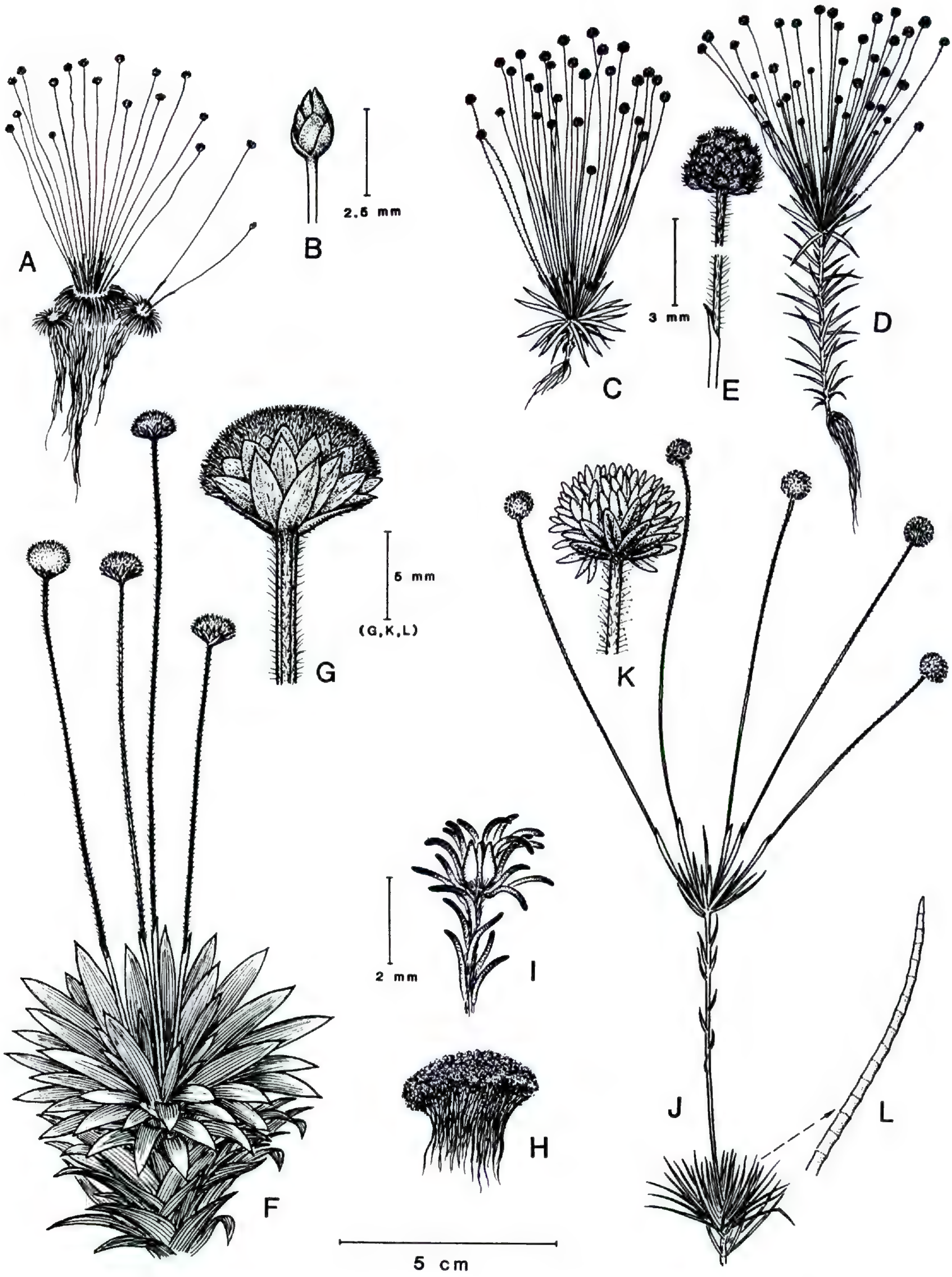

FIGURE 3. Habits of *Syngonanthus setifolius* Hensold, *Paepalanthus fasciculoides* Hensold, *P. chimantensis* Hensold, *S. acephalus* Hensold, and *S. fenestratus* Hensold. A, B. *S. setifolius* (*Liesner 3914* MO).—A. Habit.—B. Inflorescence in bud. C–E. *P. fasciculoides* (*Silva et al. 1756* MO).—C, D. Habit.—E. Inflorescence. F, G. *P. chimantensis* (*Huber 11598* MO).—F. Habit.—G. Inflorescence. H, I. *S. acephalus* (*Vareschi & Magdefrau 6789* VEN).—H. Habit.—I. Fertile branch with terminal flower. J–L. *S. fenestratus* (*Vareschi & Magdefrau 6612* VEN).—J. Habit.—K. Inflorescence.—L. Leaf. Scale bar at base applies to all habit illustrations.

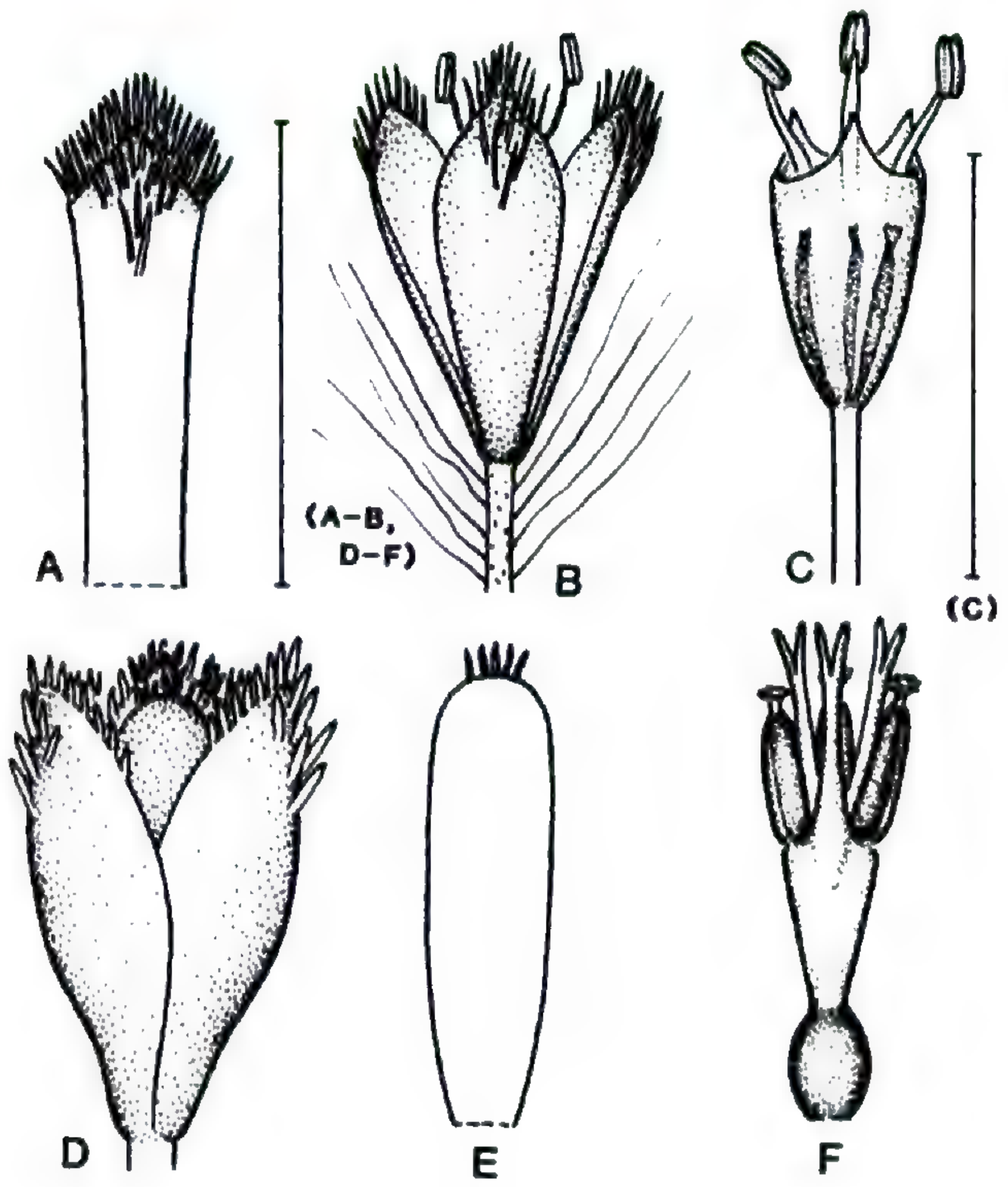

FIGURE 4. *Paepalanthus chimantensis* Hensold (*Huber & Steyermark 6971* MO). A–C. Staminate flower.—A. Floral bract.—B. Flower.—C. Flower with sepals removed. D–F. Pistillate flower.—D. Flower.—E. Petal.—F. Gynoecium. Scale bar A–B, D–F = 3 mm; scale bar C = 2 mm.

the base, sepals remaining after dispersal of fruit; petals oblong to elliptic, rounded at apex, ca. 2.7 mm long, 0.8 mm wide, glabrous or sparingly ciliate along upper margins, expanding and thickening at maturity and dispersed with the fruit. Ovary ca. 0.75 mm long, blackish, with one functional locule, the style 0.9 mm long, 3-angled and expanded above, broadest just below divergence of the appendages, where it about equals the ovary in diameter; appendages 3, ca. 0.9 mm long, fusiform-terete, smooth and blackish except for the pale papillate apex; style branches diverging slightly but distinctly above the appendages, ca. 1.0 mm long, shallowly bifid, slightly exsert. Fruit an achene.

Additional specimens examined. VENEZUELA. BOLÍVAR: Chimantá Massif, Apácara-tepui, 2,100–2,200 m, *Huber & Steyermark 7035* (VEN), *Huber et al. 8817* (NY), *Huber et al. 8823* (NY), *Steyermark 128376* (LL, MO); Chimantá Massif, C. section, 2,120 m, *Steyermark & Wurdack 750* (F, NY), *Steyermark & Wurdack 764* (F, NY); Chimantá Massif, Murey- (Eruoda-) tepui, 2,600 m, *Huber 11598* (MO).

This distinctive Chimantá Massif endemic is a member of subg. *Monosperma*. It has previously been confused with *Paepalanthus kunhardtii* Mold., *P. schomburgkii* Klotzsch ex Koern., and *Leiothrix turbinata* Gleason (see *P. turbinatus* below). It is best distinguished by its rosulate habit, glossy glabrous sharp-mucronate leaves, more or less oblong grayish involucral bracts, and the petals of the pistillate flowers which equal the sepals and are subglabrous. It has been collected in flower from January to March.

This species is unrelated to the unpublished herbarium name "Paepalanthus chimantensis," which Moldenke (1957) mentions as a synonym of *Carptotepala jenmanii* (Gleason) Mold.

Paepalanthus dichotomus Klotzsch ex Koern. in C. Martius, Fl. Bras. 3(1): 348. 1863. *Dupatya dichotoma* (Klotzsch ex Koern.) Kuntze, Revis. Gen. Pl. 2: 745. 1891. TYPE: Venezuela. Bolívar: Rué-imeru falls, *Schomburgk 899* (holotype, B not seen; F photo neg. #10597).

Paepalanthus guyanensis Klotzsch ex Koern. in C. Martius, Fl. Bras. 3(1): 347. 1863. *Dupatya guyanensis* (Klotzsch ex Koern.) Kuntze, Revis. Gen. Pl. 2: 745. 1891. TYPE: Venezuela. Bolívar: Rué-imeru falls, *Schomburgk s.n.* (holotype, B not seen). Syn. nov.

Syngonanthus savannarum Mold., Bull. Torrey Bot. Club 75: 202. 1948. *Paepalanthus savannarum* (Mold.) Mold., Phytologia 49: 293. 1981. TYPE: Guyana. Kaieteur Savanna, *Maguire & Fanshawe 23280* (holotype, NY; isotypes, F, MO). Syn. nov.

Paepalanthus steyermarkii Mold., Fieldiana, Bot. 28: 125. 1951. TYPE: Venezuela. Bolívar: Gran Sabana, between Kavanayén and Río Karuai, 1,220 m, *Steyermark 59369* (holotype, NY; isotype, MO). Syn. nov.

Syngonanthus venezuelensis Mold., Fieldiana, Bot. 28: 128. 1951. TYPE: Venezuela. Bolívar: Gran Sabana, between Kavanayén and Río Karuai, 1,220 m, *Steyermark 59347* (holotype, NY; isotypes, F, MO). Syn. nov.

Syngonanthus savannarum var. *glabrescens* Mold., Mem. New York Bot. Gard. 9: 412. 1957. *Paepalanthus savannarum* var. *glabrescens* (Mold.) Mold., Phytologia 49: 293. 1981. TYPE: Venezuela. Bolívar: Chimantá Massif, C. section, base of upper falls of Rio Tirica, *Steyermark & Wurdack 539* (holotype, NY; isotype, F). Syn. nov.

Paepalanthus apacarensis var. *humilis* Mold., Phytologia 54: 66. 1983. TYPE: Venezuela. Bolívar: Chimantá Massif, central NE sector of Chimantá-tepui, E headwaters of Caño Chimantá, *Steyermark 128164* (holotype, LL not seen). Syn. nov.

Paepalanthus dichotomus, endemic to the Gran Sabana of Venezuela and adjacent Guyana, has previously been recognized under several names, probably owing to the large variation found in pubescence, leaf texture, and peduncle elongation. However, these characters are found to vary continuously and independently of each other, and the segregation of distinct taxa within this complex is not supportable. That some of the taxa were de-

scribed in *Syngonanthus* probably owes to the tight coherence of the apices of the pistillate flower petals, which are nonetheless not truly fused. In other respects (fibrous roots, sepals tufted with trichomes, trichomes often tuberculate with ornamented internal walls, sepals of the pistillate flowers hygroscopic and thickening and recoiling to eject fruit at maturity), this species is definitely allied to *Paepalanthus*.

Paepalanthus fasciculoides Hensold, sp. nov.
TYPE: Brazil. Pará: Marabá, Serra dos Carajás, 700–750 m, *A. S. L. da Silva et al. 1756* (holotype, MO; isotype, NY). Figures 3C–E, 5.

Herba annua erecta caulescens. Folia linearia ca. 5–10 mm longa, 0.5–1 mm lata attenuata, superne hispida. Inflorescentiae multae terminaliter fasciculatae. Capitula ca. 2 mm lata, globosa. Bracteae involucrales fuscae late oblongo-obovatae, ciliatae; bracteae florales eis similes, rotundatae dense ciliatae, infra apicem abaxialiter barbatae. Sepala florum staminatorum fusca oblanceolata basi attenuata.

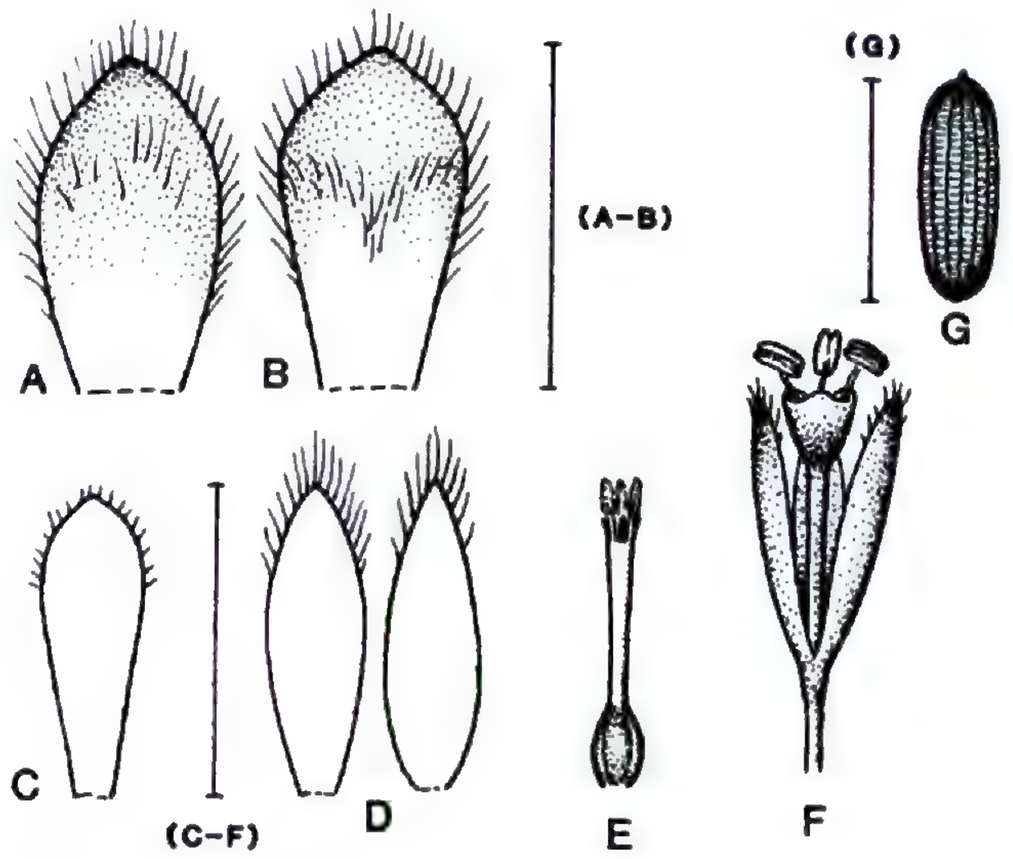

FIGURE 5. *Paepalanthus fasciculoides* Hensold (*Silva et al. 1756* MO).—A. Involucral bract.—B. Floral bract. C–E. Pistillate flower.—C. Sepal.—D. Petals.—E. Gynoecium.—F. Staminate flower.—G. Seed. Scale bar A–B = 1 mm; scale bar C–F = 1 mm; scale bar G = 0.6 mm.

Plants annuals with leafy stems up to ca. 5 cm long. Leaves dark green, ca. 5–10 mm long, 0.5–1 mm wide, longer toward stem apex, attenuate, not ampliate at base, spreading, the upper surface hispid (with short, stiff hairs). Inflorescences numerous and clustered at stem apex. Peduncle sheaths with the apex attenuate-acute and often deflexed at right angles. Peduncles ca. 2–5 cm long, pilose with long spreading hairs, green, obscurely 3-costate. Heads 2–3 mm diam., globose. Involucral bracts dark fuscous, broadly oblong-obovate, obtuse, concave to navicular, ca. 1.2–1.5 mm long, densely ciliate at upper margin and sparsely pilose in medial area on abaxial side. Floral bracts similar in size to involucral bracts, also fuscous, broadly spatulate and rounded or obtuse at apex, navicular, distinctly narrowed toward base, ciliate along upper margin and densely bearded in a V-shaped medial band below apex. *Staminate flowers*. Pedicels ca. 0.3–0.5 mm long. Sepals 3, connate at base, oblanceolate, acute, ca. 1.2 mm long, fuscous at least apically, ciliate at upper margin, enough narrowed at base so that the androphore is visible without teasing the bases apart. Corolla inserted on a very long androphore nearly equaling the sepals, the tube itself at least partially exsert from the calyx; anthers white, ca. 0.3 mm long. *Pistillate flowers*. Sepals 3, connate very briefly at base, linear-spatulate, ca. 1.0 mm long at anthesis, cream-colored, sparsely ciliate at upper margin, thickening, elongating and recoiling hygroscopically at fruiting. Petals hyaline, oblong, obtuse to acute, ciliate along the distal margin, about equaling the sepals. Gynoecium with style 2–3 times the length of the style branches; style branches simple, about twice the length of the filiform appendages. Seeds oblong, 0.6 mm long and less than half as wide, yellow-brown, the testa with prominent longitudinal striations.

Additional specimens examined. VENEZUELA. BOLÍVAR: Cerro Cotorra (El Vigía), south side of Río Paragua between La Paragua and San Pedro de Las Bocas, 600 m, 5 Aug. 1960, *Steyermark 86888* (VEN). BRAZIL. PARÁ: Marabá, Serra dos Carajás, solo com cascalho de pedras, *M.G. Silva 2920* (NY); Marabá, Serra Norte, Carajás, N1, on canga outcrop, May 1986, *Marli et al. 70* (SPF).

Paepalanthus fasciculoides is distinguished from its closest relative, *Paepalanthus fasciculatus*, by the dark brown obovate to spatulate involucral and floral bracts with entire upper margins, the dense subapical bearding of the floral bracts, and the narrow oblanceolate sepals. In *P. fasciculatus*, the bracts are buff-colored, usually conspicuously mucronate or apiculate, and at least the floral bracts are usually rather broadly obtrullate with a flattish upper margin. Instead of being densely bearded, they are generally sparsely pilose in one medial or two submedial bands. The sepals of the staminate flowers in *P. fasciculatus* are more or less broadly elliptic, the lateral margins overlapping each other and concealing the basal part of the corolla. The two species may also be ecologically distinct, the rarer *P. fasciculoides* being found only on rocky soils and canga in low mountains of Amazonian Brazil and Venezuelan Guayana, while *P. fascicu-*

latus is a common species of sand savannas at low altitudes.

Paepalanthus major (Mold.) Hensold, comb. et stat. nov. *Paepalanthus convexus* var. *major* Mold., Phytologia 15: 463. 1968. TYPE: Brazil. Amazonas: Serra Pirapucú, Rio Negro, Rio Cauaburí, Rio Maturacá, *Silva & Brazão 60926* (holotype, NY; isotypes, NY (2)).

Paepalanthus fulgidus var. *zuloagensis* Mold., Phytologia 23: 211. 1972. TYPE: Venezuela. Bolívar: Cerro de la Neblina, Planicie de Zuloaga, Río Titirico, *Steyermark 103839* (holotype, NY; isotype, NY). Syn. nov.

Paepalanthus major of Cerro de la Neblina is distinguished from *P. convexus* Mold. of Cerro Duida by its acaulescent to short-caulescent habit, its larger leaves with a smooth (not sulcate) upper epidermis, and its solitary robust inflorescences with peduncle sheaths far surpassing the leaves. Its closest allies are the sympatric *P. gleasonii* Mold., and probably *P. squamuliferus* Mold., the latter of tepui summits in the Gran Sabana.

It is distinguished (imperfectly) from *P. gleasonii* by its usually shorter stems, more sharply cuspidate leaves, and especially by the sericeous upper leaf surface, lack of well-defined cilia, and the slightly revolute margins. In *P. gleasonii*, the leaves are bluntly cuspidate, densely short-ciliate, and occasionally also hirsute adaxially at the apex, but otherwise early glabrate on both surfaces, and the margins flat in drying.

It differs from *P. squamuliferus* also by the sharply acute leaf apices, as well as by the acute to acuminate involucral bract apices. In *P. squamuliferus*, the leaves are subacute to rounded, but never sharp-cuspidate, and the involucral bracts are usually obtuse to rounded.

"*Paepalanthus fulgidus* var. *zuloagensis*," also from Neblina and known only from the type, appears to be a dwarf form of *P. major*, with smaller leaves and heads. I am provisionally placing it in synonymy pending the availability of further material.

Paepalanthus convexus, with its numerous small inflorescences, peduncle sheaths approximately equaling the leaves, and leaves strongly sulcate-ribbed on the upper surface, is a more distant relative probably derived from *Paepalanthus sulcatus* Hensold (originally described from Cerro de la Neblina as *P. stegolepoides* var. *acutalis* Mold.).

Paepalanthus parvicephalus (Mold.) Hensold, comb. et stat. nov. *Paepalanthus convexus* var. *parvicephalus* Mold., Phytologia 52: 19. 1982. TYPE: Venezuela. Amazonas: Cerro Marahuaca-Fhuif, 2,330–2,460 m, *Steyermark et al. 126100* (holotype, LL not seen).

Although both *P. parvicephalus* of Cerro Marahuaca and *P. convexus* of nearby Cerro Duida share a long-stemmed, clambering habit, they differ strongly in leaf form and inflorescence arrangement. In *P. convexus*, the leaves are acute, with the veins inscribed on the upper surface, and the whole leaf strongly reflexed at maturity, while in *P. parvicephalus*, the leaves are obtuse, the veins obscurely if at all inscribed above, and the leaves divergent, not strongly reflexed at maturity. In addition, *P. convexus* is unique for its numerous small, short-pedunculate inflorescences. Although the two taxa appear closely related, *P. sulcatus* appears on morphological and geographic grounds to be a possible common ancestor to both, even to the extent of intergrading with *P. parvicephalus* at the southern end of its range. *Paepalanthus parvicephalus* is therefore elevated to specific status in order to avoid probable misrepresentation of relationships.

Paepalanthus parvicephalus var. **wurdackii** (Mold.) Hensold, comb. nov. *Paepalanthus perplexans* var. *wurdackii* Mold., Mem. New York Bot. Gard. 8: 98. 1953. TYPE: Venezuela. Amazonas: Serranía Parú, Río Parú, Caño Asisa, 2,000 m, *Cowan & Wurdack 31141* (holotype, NY).

This taxon, native to the Serranía Parú, appears closely related to and probably derived from *P. parvicephalus* var. *parvicephalus* of Cerro Duida. It differs from this variety primarily in its smaller heads (4.5–5 mm diam. vs. 6.5–8 mm in var. *parvicephalus*). It is distinguished from *P. schomburgkii* Mold. of the Gran Sabana by the following characteristics: leaves ligulate, i.e., linear and subacute to obtuse, cuspidate, and densely long-ciliate at base, the venation not pellucid; involucral bracts of the lower series thickened and red-brown at base. *Paepalanthus schomburgkii* is characterized by broader leaves straight-tapered to an acute apex, not distinctly cuspidate, often long-ciliate, but the cilia not densely crowded at the base, and the venation pellucid. The involucres of *P. schomburgkii* are generally of a finer, herbaceous texture, and the bracts of the lower series not distinctly thickened as above.

Paepalanthus tortilis (Bong.) Koern. in C. Martius, Fl. Bras. 3(1): 354. 1863. *Eriocaulon*

tortile Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1: 624, t. 49. 1831. *Dupatya tortilis* (Bong.) Kuntze, Revis. Gen. Pl. 2: 746. 1891. TYPE: Brazil. Bahia: in arenosis humidis propre Ilheos, *Riedel s.n.* (LE not seen).

Paepalanthus salticola Herzog, Feddes Repert. Spec. Nov. Regni Veg. 29: 207, pl. 121, figs. i–l. 1931. SYNTYPES: Brazil. Alto Amazonas: Tiquié, Uira Poço, Uferwald, *Luetzelburg 23906* (M); Paporí, Trinidade, am Fall, *Luetzelburg 23912* (M, F photo neg. #18725). Syn. nov.

Paepalanthus tatei Mold., Brittonia 3: 158. 1939. TYPE: Venezuela. Bolívar: Auyán-tepui, 2,200 m, *Tate 1326* (holotype, NY). Syn. nov.

Paepalanthus killipii Mold., Bull. Torrey Bot. Club 68: 67. 1941. TYPE: Colombia. Santander Sur: E cordillera, Mesa de los Santos, *Killip & Smith 15299* (holotype, US not seen; isotype, F). Syn. nov.

Paepalanthus maguirei Mold., Bull. Torrey Bot. Club 75: 198. 1948. TYPE: Surinam. Tafelberg, North Ridge Cascade, Savanna I, *Maguire 24670* (holotype, NY; isotype, F). Syn. nov.

Paepalanthus tortilis owes its lengthy synonymy to wide variation in vegetative size and habit of flowering specimens. Ruhland's (1903) description of the species contains no measurements, but indicates a short or scarcely elongate stem with leaves clustered toward the apex. This is generally true of the material from eastern and Amazonian Brazil, as well as more depauperate collections from Guayana. However, much of the more recent collections from the Andes, as well as from tepui formations in Venezuela, are much more robust, often with long, uniformly leafy stems, but even in these areas, all gradations in size are found to occur, making division into discrete varieties or forms untenable. In Guayana alone, plants range from tiny rosettes with leaves 8 mm long and 1 mm wide, and peduncles of 5 cm, to clambering long-stemmed herbs with leaves 6 cm long and 8 mm wide, and peduncles up to 25 cm. According to Stützel (pers. comm.), greenhouse-grown plants in Ulm, all propagated from a single plant of Auyán-tepui, Venezuela, tended to flower in December regardless of plant age and size, resulting in flowering specimens of widely varying sizes, from 2 to 25 cm tall, and with leaf sizes varying widely as in herbarium material. Inflorescence size varies by a smaller factor, with heads ranging from 2.5–6 mm diam.

I am not entirely comfortable explaining all the variation in *P. tortilis* on the basis of age and environmental factors. For example, although large caulescent forms are known from eastern Brazil, they seem to be much rarer there and also localized. (*Paepalanthus obtusifolius* (Steudel) Koern. of Bahia is a probable example.) However, even if a genuine taxonomic distinction exists between the larger and smaller forms, the overlap in size ranges would be expected to be too great to allow identification on the basis of size alone.

Within Venezuela, plants of La Gran Sabana, regardless of size, are firmer in texture and have more rounded leaf margins than plants of Amazonas or the Andes. Specimens of particular interest are *Maguire 31718* (Serranía Guanay), a "gigas" plant with inflorescences to 8 mm diam., and *Liesner 19729* (El Pauji, Bolívar), a long-stemmed plant with large leaves, firm, ciliate involucral bracts, uniformly dark-colored flowers, and large papillate appendages. This contrasts with the fine herbaceous involucres, sepals streaked red-brown along the midvein, and filiform appendages of typical *P. tortilis*. The collection may represent a new species or a hybrid, but additional material is desirable.

Paepalanthus turbinatus (Gleason) Hensold, comb. nov. *Leiothrix turbinata* Gleason, Bull. Torrey Bot. Club 58: 331. 1931. TYPE: Venezuela. Amazonas: Cerro Duida, *Tate 775* (holotype, NY).

This species of Cerro Duida is a member of subg. *Monosperma*. It is characterized by its clumping habit, its leaves pilose on both surfaces and smooth above (the veins not inscribed), and by the floral bracts bearded abaxially with a naked long-acuminate apex.

Paepalanthus yapacanensis (Mold.) Hensold, comb. nov. *Syngonanthus yapacanensis* Mold., Mem. New York Bot. Gard. 8: 102. 1953. TYPE: Venezuela. Amazonas: Cerro Yapacana, Río Orinoco, *Maguire et al. 30782* (holotype, NY; isotypes, F, MO).

Paepalanthus yapacanensis, which does not have the medially connate petals of the pistillate flower found in *Syngonanthus*, is closely related to *P. dichotomus* Klotzsch ex Koern. and its allies, including *P. aristatus* Mold., with which it is sympatric on white sand savannas in Amazonas. It shares with these species a mat-forming, dichotomously branching habit, black wiry roots, linear obtuse leaves with silvery appressed cilia toward the apex, leathery peduncles abruptly constricted at the apex, involucral bracts with brittle hyaline margins, and a similar floral morphology. The numerous series of pale subhyaline involucral bracts suggest a superficial similarity with *Syngonanthus nitens* (Bong.) Ruhl. and *S. xeranthemoides* (Bong.)

Ruhl., which probably accounts for its original placement in that genus. Two varieties occur, both endemic to Amazonas, Venezuela, and the following is also transferred to *Paepalanthus*.

Paepalanthus yapacanensis var. **hirsutus** (Mold.) Hensold, comb. nov. *Syngonanthus yapacanensis* var. *hirsutus* Mold., Phytologia 36: 51. 1977. TYPE: Venezuela. Amazonas: 12–40 km from San Fernando de Atabapo, on road to Sta. Bárbara, *Gentry & Tillett 10869* (holotype, LL not seen; isotypes, MO, VEN).

Additional specimens examined. VENEZUELA. AMAZONAS: sandy bana 12 km N of San Carlos, 100–120 m, 6 Feb. 1977, *Morillo & Villa 5406* (MO, VEN); on white sand 1 km E of Maroa, 125 m, 20 Apr. 1970, *Steyermark & Bunting 102837* (LL, MO, VEN).

SYNGONANTHUS

Syngonanthus acephalus Hensold, sp. nov. TYPE: Venezuela. Amazonas: Selva secundaria de San Carlos del Río Negro, 25 Jan. 1958, *Vareschi & Magdefrau 6789* (holotype, VEN; isotype, MO). Figures 3H, I, 6.

Herba perennes pulvinos formantes, habitu similis musco. Folia linearia, 1–2 mm longa, 0.2 mm lata. Flores singulatim vel binatim ad apices caulium foliosorum portati. Pedunculi et involucra carentia. Flores dimeri bisexuales actinomorphi; sepala ovata glabra; petala basin versus carnosa in medio connata; filamenta basi petalorum affixa.

Perennials forming branched mosslike mats. Roots abundant, white, spongy, slightly larger in diameter than the leaves. Stems ca. 1 cm long, fine, branched, soft-pilose. Leaves linear to ligulate, obtuse, 1–2 mm long, 0.2 mm wide, membranous to coriaceous, gently recurved-spreading, glabrous. Inflorescences reduced to 1–2 flowers, these terminal on unspecialized leafy branches and subtended by dense tufts of hair. Floral bracts present, though sometimes green and undifferentiated from foliage leaves, occasionally brownish. Peduncles undeveloped. Flowers bisexual, actinomorphic. Sepals 2, free, 1–1.3 mm long, triangular-ovate, carinate, cupped at base around locule and seed, the apex often fleshy-subterete, simulating apex of foliage leaves, cream-colored or greenish, glabrous. Petals oblanceolate to obtrullate, acute, fleshy in lower half, membranous above, the upper margins connate, with a row of stout hairs overlaying the area of fusion. Filaments adnate to petals in lower half; anthers cream, ca. 0.15 mm long. Style ca. 0.35 mm long; appendages papillose, filiform or narrowly infundibular, ca. 0.3 mm long; style branches simple, about equaling the appendages. Seeds dark red-brown, ca. 0.4 mm long, 0.3 mm wide, longitudinally striate, with fine less conspicuous transverse striations.

Syngonanthus acephalus shares with *S. amazonicus* Mold. 2-merous, bracteate, bisexual flowers with the petals connate at the upper margins and fleshy below, and with the staminal filaments adnate to the corolla. However, the very reduced 1–2-flowered inflorescence of *S. acephalus*, in which peduncles and involucres are lacking, is to my knowledge not found elsewhere in the Eriocaulaceae.

This species occurs on sandy sites at low elevations in southwestern Amazonas, where it is sympatric with *S. amazonicus*.

Because of its mosslike habit, this species had previously been identified as sterile material of *Syngonanthus vareschii* Mold. (See discussion of *S. vareschii*.)

Syngonanthus duidae var. **humilis** Hensold, var. nov. TYPE: Venezuela. Bolívar. Summit of Kukenán-tepui, 2,550 m, *Liesner 23134* (holotype, MO).

Folia 0.4–0.6 cm longa. Vaginae pedunculorum 0.8–1.0 cm longae. Pedunculi 2–7 cm longi. Capitula 3–6.5 mm lata.

Perennials forming low dense colonies. Stems up to 1 cm long. Leaves linear, 0.4–0.6 cm long, the upper surface appressed-hairy to nearly glabrous. Peduncle sheaths 0.8–1.0 cm long; peduncles 2–7 cm long. Heads 3–6.5 mm diam.

Additional specimens examined. VENEZUELA. BOLÍVAR: summit of Roraima, *Delascio & Brewer 4745* (VEN); plateau below summit of Uei-tepui (Cerro del Sol), W sector, above valley of Río Arabapó, *Huber 10.030* (MO).

This variety, which is endemic to the Roraima formation in the southeastern part of the Gran Sabana, differs from var. *duidae* in its reduced leaves and peduncles. Variety *duidae*, which is widespread elsewhere in the Gran Sabana and also at high altitudes in Amazonas, typically has leaves 1–4 cm long, and peduncles up to 35 cm long.

Syngonanthus fenestratus Hensold, sp. nov. TYPE: Venezuela. Bolívar: Raudales de Canaima, 1 Oct. 1958, *Vareschi & Magdefrau 6612* (holotype, VEN). Figures 3K–J, 7.

Herba caule primario perbrevi rosulata; ramo solitario erecto parce folioso ad apicem 3–5 inflorescentias efferenti. Folia basalia linearia acuta fenestrata glandulosa

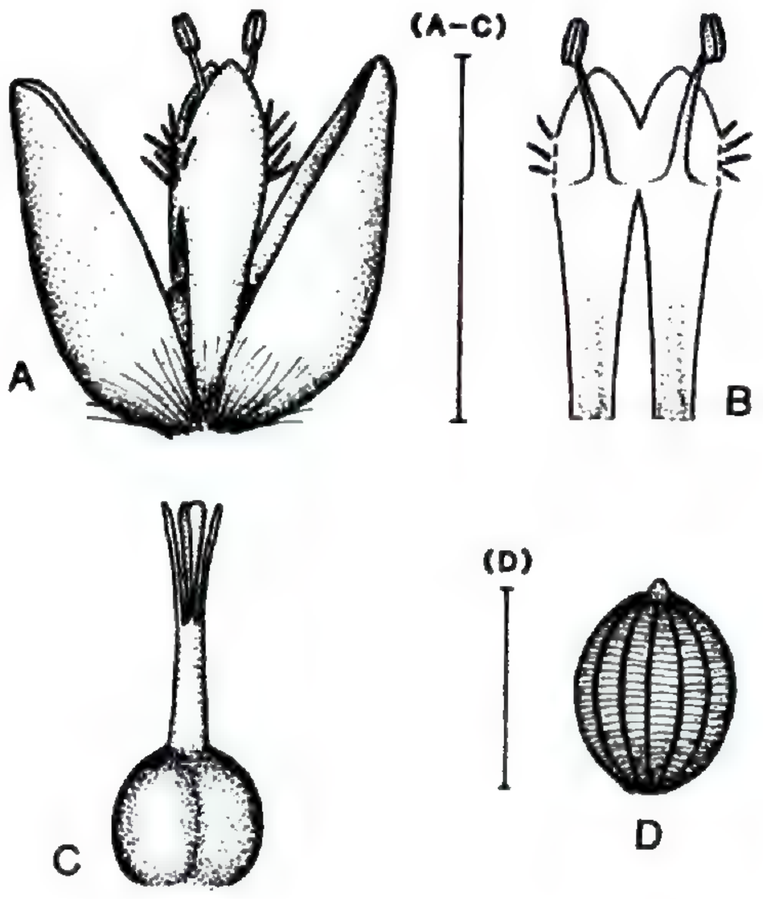

FIGURE 6. *Syngonanthus acephalus* Hensold (*Vareschi & Magdefrau 6789* VEN).—A. Flower (bisexual) with sepals spread open.—B. Corolla split open along one side.—C. Gynoecium.—D. Seed. Scale bar A–C = 1 mm; scale bar D = 0.4 mm.

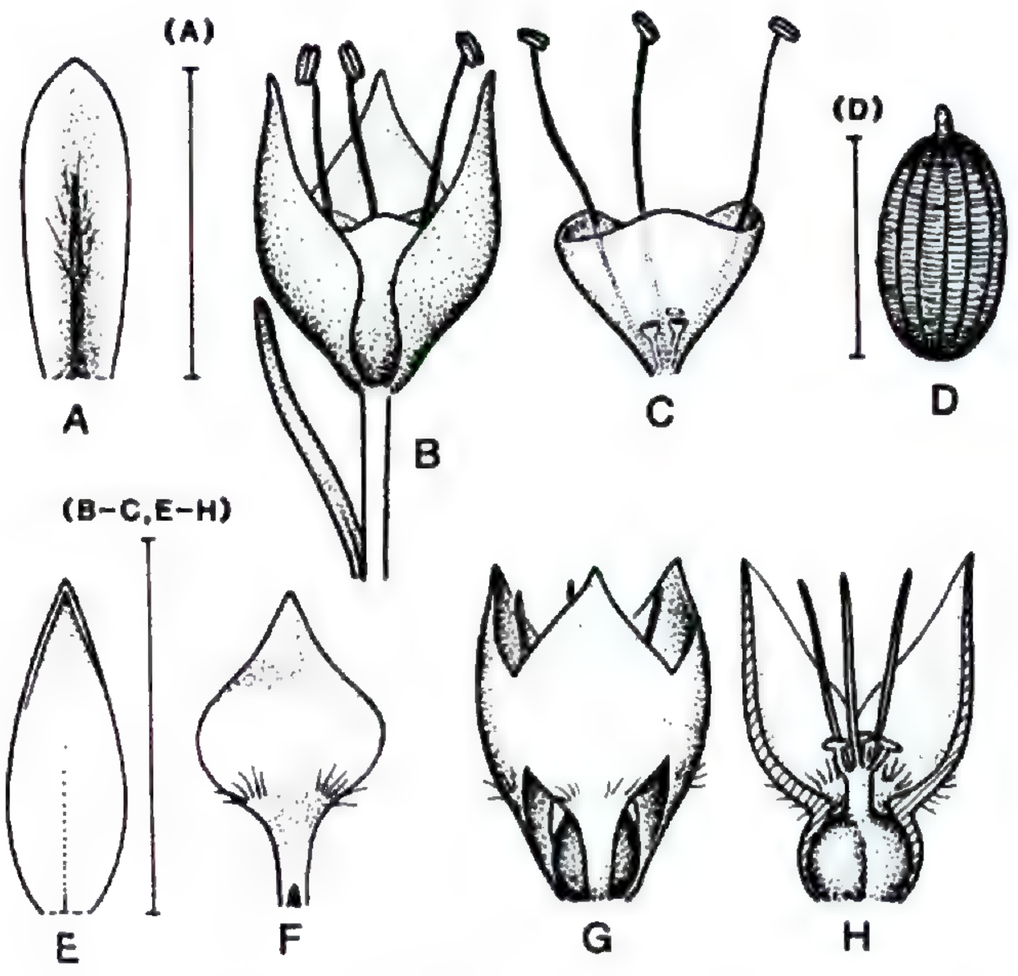

FIGURE 7. *Syngonanthus fenestratus* Hensold (*Vareschi & Magdefrau 6612* VEN).—A. Involucral bract. B, C. Staminate flower.—B. Flower with floral bract.—C. Corolla with sepals removed.—D. Seed. E–H. Pistillate flower.—E. Sepal, adaxial view.—F. Petal of flower after anthesis (margins free), adaxial view.—G. Flower at anthesis with sepals removed.—H. The same, with one petal removed, showing corolla clasping style. Scale bar A = 2 mm; scale bar B–C, E–H = 3 mm; scale bar D = 0.6 mm.

1.5–4 cm longa. Folia caulina anguste lanceolata 5–8 mm longa. Pedunculi 6-costata glandulosa. Capitula ca. 6–7 mm lata. Bracteae involucrales oblongae subhyalinae plerumque secus costam castaneae. Bracteae florales longitudine ½ florum aequantes. Flores actinomorphi; sepala elliptica acuta; corollae carnosae, lobis non-involutis, eis florum pistillatorum acuminatis.

Plants rhizomatous herbs, producing a basal rosette and a solitary erect (fertile) branch bearing an umbel of inflorescences at the apex. Roots white, spongy. Basal leaves linear, acute, 1.5–4 cm long, 0.5–0.7 mm wide, membranous, flat or subterete, fenestrate, glandular-hairy, the midvein prominently thickened. Fertile branch 3–6.5 cm long, yellow-green when young, dark reddish brown at maturity, sparingly foliose, the leaves spirally arranged, lance-linear, acute, glandular, ca. 5–8 mm long, or those clustered at apex up to 13 mm long. Inflorescences 3–5 per umbel. Peduncle sheaths 1.5–2.5 cm long, densely glandular-hairy, lax, subacute to obtuse with a narrow sinus ca. 5 mm deep; peduncles 7–13 cm long, 6-costate, glandular toward apex. Heads globose at maturity, 6–7 mm diam.; involucral bracts in ca. 2 series, oblong, obtuse, ca. 2–2.5 mm long, hyaline, reddish brown, especially along the midvein, the margins sometimes colorless, glabrous, or sometimes pilose abaxially but not along margins, becoming reflexed and lost from view upon maturation of head. Floral bracts present, linear, subacute, whitish, about half-equaling the flowers. *Staminate flowers.* Sepals 3, briefly connate at base, elliptic, acute, carinate, ca. 2.1 mm long, cream-colored, glabrous. Corolla tubular, broadly infundibular, about half the length of the sepals or less, very fleshy, the lobes nearly obsolete, noninvolute. Stamens with filaments free, strongly exsert, about equaling the sepal apices; anthers white, ca. 0.2 mm long. Pistillodes present, simulating gynoecial appendages. *Pistillate flowers.* Sepals 3, free, ca. 2.9 mm long, always cream-colored, otherwise as in staminate flowers. Petals connate at their upper margins, but separating after anthesis, broadly spatulate-acuminate, with a narrow claw at the base, ca. 2.7 mm long, very fleshy, noninvolute, with a cushionlike thickening in the middle which rests against the style, pilose on both surfaces near margins at base of fusion zone. Style very short; appendages infundibular, reddish, with a white-papillose rim; style branches simple, about equaling the petals. Seeds ellipsoidal, with a wart-like protrusion at the funicular end, ca. 0.6 mm long and 0.3 mm wide, the outer epidermis longitudinally striate, the striae swelling when wet and breaking apart to form short hairlike processes.

Additional specimens examined. GUYANA. RUPUNUNI DISTR.: Chaakoitou, near Mountain Point, just south of Kanuku Mountains, 2°56′N, 59°40′W, *Maas & Westra 4050* (MO, NY).

This species has been confused with *Syngonanthus bisumbellatus* (Steudel) Ruhl., with which it shares small stature and sparingly leafy aerial stems with spirally arranged leaves. *Syngonanthus fe-*

nestratus can be easily distinguished by its larger heads, oblong brownish involucral bracts and by the actinomorphic flowers with fleshy corollas. These floral characters, together with the fenestrate leaves, suggest alliance of the species with sect. *Carphocephalus* (Koern.) Ruhl. and perhaps especially with the widespread amphibious species *S. anomalus* (Koern.) Ruhl.

Syngonanthus humboldtii var. **parvus** (Mold.) Hensold, comb. nov. *Syngonanthus allenii* var. *parvus* Mold., Mem. New York Bot. Gard. 8: 99. 1953. TYPE: Venezuela. Amazonas: Puerto Ayacucho, *Maguire et al. 29238* (holotype, NY).

Syngonanthus humboldtii var. *parvus* is a reduced form of the widespread *S. humboldtii*, lacking verticils of leaves on the aerial stem, and limited to laja formations in the vicinity of Puerto Ayacucho, Amazonas, Venezuela. In these areas it is sympatric with var. *humboldtii*, with which it shares acute to subacute involucral bract apices, the absence of floral bracts, and acute glabrous sepal apices. This contrasts with *S. allenii* Mold. of Colombia, which is characterized by aristate involucral bracts, the presence of floral bracts, and acuminate ciliate sepal apices.

Syngonanthus macrocephalus (Mold.) Hensold, comb. et stat. nov. *Syngonanthus humboldtii* var. *macrocephalus* Mold., Mem. New York Bot. Gard. 8: 101. 1953. TYPE: Venezuela. Amazonas: Cerro Sipapo, North Mountain, 5,000–6,000 ft., *Maguire & Politi 27649* (holotype, NY).

This rare endemic of the Cerro Sipapo (northwestern Amazonas, Venezuela) is probably not closely related to *S. humboldtii* (Kunth) Ruhl., but its true affinities are difficult to interpret. Like *S. humboldtii*, its inflorescences are disposed in umbels arising from the apex of fertile aerial branches. It differs from *S. humboldtii* in that these branches are naked and usually relatively short in comparison to the peduncles, the inflorescences are few (1–5), and the heads are larger, between 5 and 10 mm diam. In addition, the peduncles are 5–6-costate, the involucral bracts are lance-acute, and the bracts and perianths of the inflorescence are suffused with coppery brown. In all of these respects, it is more similar to *S. procerus* Mold. of Central Brazil.

The type specimen is on a mixed sheet with *S. duidae* Mold., which although it lacks the stem dimorphism and involucre color of *S. macrocephalus*, bears a strong superficial resemblance to this species.

Syngonanthus minutus (Mold.) Hensold, comb. nov. *Paepalanthus minutus* Mold., Brittonia 3: 158. 1939. TYPE: Venezuela. Bolívar: Auyán-tepui, 2,200 m, *Tate 1328* (holotype, NY).

This rare species of *Syngonanthus*, endemic to Auyán-tepui and known only from the type, was originally described in *Paepalanthus* due to the lack of fusion of the petals in the pistillate flower. However, considering a wide range of characters, its closest affinities appear to lie with *Syngonanthus*, in particular *S. simplex* (Miq.) Ruhl. and *S. gracilis* (Bong.) Ruhl., both of which also occur in Venezuelan Guayana, though apparently not at altitudes higher than 1,500 m. The small size, rosulate habit, aerenchymatous roots, acicular 1-veined leaves, glabrous inflorescences, and gold subhyaline bracts and sepals of *S. minutus* immediately suggest both these species, as do particularly the falcate-asymmetric calyces of the staminate flowers. Also like these species, *S. minutus* lacks floral bracts, and has corollas in the staminate flowers raised on an androphore, stigmas undivided, and small filiform stylar appendages.

It is true that the 2-merous flowers with petals free in both sexes make the species unique as far as we know in *Syngonanthus*. However, in *S. gracilis* and *S. minutus* the posterior sepal is reduced relative to the two falcate anterior ones, and it is not difficult to imagine its complete loss in a reduction series, together with corresponding reduction in other floral parts.

The simultaneous loss of fusion in the petals of both staminate and pistillate flowers is an uncommon condition in *Paepalanthus* and *Syngonanthus*, and thus not informative with respect to generic alliance. Consistently free petals in staminate and pistillate flowers are found in *Leiothrix fluitans* (Mart.) Ruhl. and *Rondonanthus* (*Paepalanthus*) *capillaceus* (Klotzsch ex Koern.) Hensold & Giulietti, two rheophytic species whose closest relatives have petals fused in at least the staminate flowers. (See also the discussion of *Syngonanthus jenmanii* (Gleason) Giulietti & Hensold, Ann. Missouri Bot. Gard. 78: 441–464. 1991.) Free petals in staminate flowers of *Paepalanthus* subg. *Xeractis* occur sporadically as a developmental aberration (Hensold, unpublished data). Similar aberrations in *Syngonanthus* would presumably affect pistillate flower corollas as well. Thus, it may be that the loss of petal fusion in *S. minutus* is a developmental abnormality associated

with environmental stress (high altitude) or selection for the reduction of flower parts. In any event, the close apparent relationship between this species and *S. simplex* and allies, together with the presence of aerenchymatous roots and the absence of floral bracts, both characters not known to occur in *Paepalanthus*, suggests that the species is much more comfortably accommodated in *Syngonanthus* sect. *Dimorphocaulon* than in *Paepalanthus*.

Syngonanthus ottohuberi Hensold, nom. et stat. nov. *Syngonanthus similis* var. *venezuelensis* Mold., Phytologia 45: 209. 1980. TYPE: Venezuela. Amazonas: between Caño Cotúa and the W base of Cerro Yapacana, *Huber 1633* (holotype, LL not seen).

Syngonanthus densifolius var. *venezuelensis* Mold., Phytologia 48: 291. 1981. TYPE: Venezuela. Amazonas: on S bank of the Caño Yagua ca. 15 km upstream from its mouth, *Huber & Tillett 2918* (holotype, LL not seen; isotype, VEN).

Because this species was originally described as a variety with only a very short diagnosis, a full description is given here.

Plants perennials producing basal rosettes and a solitary, erect fertile branch bearing an umbel of inflorescences at its apex. Roots with a spongy white cortex and a wiry black fibrous core. Leaves of rosette linear, sharply acute to aristate, 2.2–4.5 cm long, 1–1.5 mm wide, coriaceous, striate below, smooth above, flat to revolute-canaliculate upon drying, glabrous. Fertile branch leafless except at apex, 6–12 cm long, blackish, shiny, glabrous or nearly so; involucral leaves subtending umbel lanceolate-acute, 2.5–3.0 cm long, 0.7 mm wide, striate, pubescent with spreading hairs. Inflorescences 3–10 per umbel. Peduncle sheaths 3–4 cm long, firm, pubescent with spreading hairs, the apex sharply acute with a rounded sinus. Peduncles 20–27 cm long, 3-costate, slightly ampliate at the apex, pubescent with spreading hairs and usually glabrate. Heads 7–7.5 mm diam., broadly turbinate. Involucral bracts in about 4 series, reddish gold, becoming grayish with age, subhyaline, glabrous, the outermost ovate, the inner oblong to oblong-oblanceolate, rounded, the largest ca. 2.5 mm long, enclosing but not surpassing the head. Floral bracts present, linear, nearly equaling the flowers, glabrous. *Staminate flowers.* Pedicels 0.5–0.9 mm long. Sepals 3, free, narrowly oblong-elliptic, 2.1–2.3 mm long, 0.4–0.5 mm wide, white. Corolla narrowly infundibular, about equaling the sepals, membranous, glabrous, the androphore very short. *Pistillate flowers.* Pedicel ca. 0.2 mm long. Sepals ca. 2.5 mm long, otherwise similar to those of the staminate flowers. Floral axis densely hairy between insertion of sepals and petals. Petals narrowly oblanceolate, connate from middle nearly to the apex, about equaling sepals, membranous, cream or tinged with reddish gold, glabrous. Style ca. 0.25 mm long; appendages ca. 0.5 mm long; style branches very fine, hairlike, adhering to the petals.

Additional specimens examined. VENEZUELA. AMAZONAS: Canaripó, S margin of lower Río Ventuari, 20 km E of confluence with Río Orinoco, *Huber 1905* (LL, NY, VEN); base of Cerro Yapacana, *Thomas & Rogers 2592* (NY).

Syngonanthus densifolius Silveira and *S. similis* Ruhl. are both described from the Serra do Espinhaço of Minas Gerais, Brazil, and neither is similar enough to *S. ottohuberi* to allow treatment of the latter as a variety. *Syngonanthus similis*, with a more compact habit, 2–5 aerial branches, whitish involucral bracts surpassing the disc, and floral bracts lacking, appears more closely related to *S. umbellatus* (Lam.) Ruhl. and *S. reclinatus* (Koern.) Ruhl.

I have not seen the type of *S. densifolius*, but the description indicates that it is also a more compact plant, with chartaceous, obtuse leaves and much shorter, glandular-hairy peduncles, with the inner involucral bracts lanceolate, recurved, and abaxially pilose, and the sepals also pilose.

The species is named for Otto Huber, distinguished Venezuelan botanist who collected the type, and has otherwise made extensive contributions to knowledge of the sand savannas of Venezuelan Amazonas.

Syngonanthus pakaraimensis var. **rivularis** (Mold.) Hensold, comb. et stat. nov. *Syngonanthus rivularis* Mold., Mem. New York Bot. Gard. 9: 411–412. 1957. TYPE: Venezuela. Bolívar: Chimantá Massif, C. section, headwaters of Rio Tírica, 2,120 m, *Steyermark & Wurdack 792* (holotype, NY; isotype, F).

Syngonanthus pakaraimensis Mold. is an abundant, widely varying and probably widely hybridizing species of the Gran Sabana. Although some variation exists between all populations of the tepui summits, the Chimantá population is the only one in which floral bracts are present and the involucral bracts relatively large and firm, slightly surpassing the disc, and reflexing somewhat at maturity. I have chosen to recognize it at the varietal level for the following reasons. First, the readily

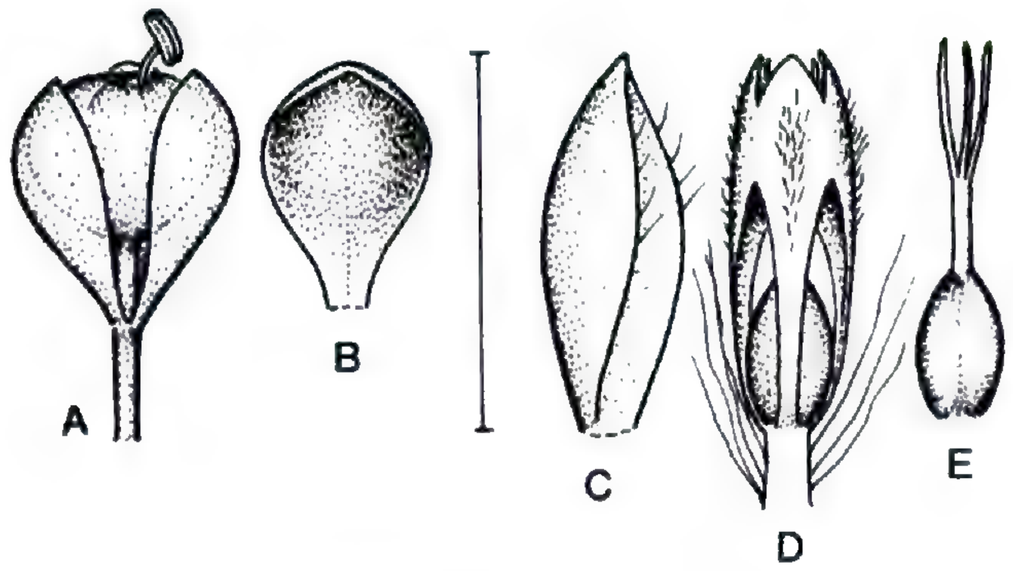

FIGURE 8. *Syngonanthus setifolius* Hensold (*Maguire & Politi 28035* NY). A, B. Staminate flower.—A. Flower.—B. Sepal, adaxial view. C–E. Pistillate flower.—C. Sepal.—D. Flower with sepals removed.—E. Gynoecium. Scale bar = 8 mm.

apparent difference between the taxa is small, especially in relation to the large amount of variation in var. *pakaraimensis* itself over its range. Second, the geographic relationship between the taxa is that considered typical of varieties. Variety *pakaraimensis* occurs on tepui summits to all sides of Chimantá but is absent from that tepui, where it is replaced by var. *rivularis*. Third, var. *rivularis* is in several respects intermediate between *S. pakaraimensis* and *S. tiricensis* Mold., another Chimantá endemic, giving reason to suspect a hybrid origin.

Syngonanthus setifolius Hensold, sp. nov. TYPE: Venezuela. Amazonas: bana on white sand, 9 km NE of San Carlos de Río Negro, 120 m, *Liesner 3857* (holotype, MO; isotype, LL). Figures 3A, B, 8.

Herba rosulata caespitosa. Folia filiformia 0.5–4 cm longa et 0.2–0.4 mm lata juventute albo-villosa. Inflorescentiae solitariae vel plures invicem sequentes. Capitula 2–2.5 mm lata. Bracteae involucrales pallidae glabrae; proximales breviter acuminatae, costis incrassatis; bracteae florales nullae. Flores staminati: sepala 3 late obovata interdum illa lateralia leviter falcata. Corollae carnosae late infundibulares lobis involutis. Flores pistillati: sepala ovato-acuminata, infra apicem ciliata. Appendices nullae.

Plants rosulate perennials. Roots spongy, white, abundant, less than 0.25 mm diam. Leaves filiform-tapered, obtuse, 0.5–4 cm long, ca. 0.2–0.4 mm wide, membranous to subterete, often recurved, the upper surface appressed-hairy or glabrate, the lower often with appressed malpighian hairs along the single prominent central vein, the entire rosette tufted with white hairs at the center. Inflorescences solitary to numerous and then produced sequentially. Peduncle sheaths green, acute at apex, coarsely pubescent with appressed hairs and sometimes also glandular-hairy. Peduncles 2.5–10 cm long, very fine, 3-costate, pubescent as the sheaths. Heads 2–2.5 mm diam. Involucral bracts white to gold, glabrous, at least the outer commonly short-acuminate with a thickened midrib, the upper oblong or obovate-rounded; floral bracts absent. *Staminate flowers.* Pedicels ca. 0.25 mm long. Sepals 3, free or sometimes irregularly fused, broadly obovate, slightly cucullate, obtuse, sometimes the two lateral slightly falcate-asymmetrical, ca. 0.5–0.6 mm long, white, glabrous. Corollas broadly infundibular and raised on an androphore, the androphore ca. 0.2 mm long, the corolla tube ca. 0.4 mm long, slightly surpassing the sepals, fleshy and bulbous, white, glabrous, involute. *Pistillate flowers.* Pedicels ca. 0.2 mm long. Sepals free, ovate, acute to acuminate, carinate, caducous, ca. 0.8 mm long, white, ciliate below the apex. Petals connate above, narrowly spatulate, about equaling the sepals, pilose abaxially below the apex. Style about equaling style branches in length; style branches simple; appendages lacking. Seeds longitudinally striate.

Additional specimens examined. VENEZUELA. AMAZONAS: Río Atabapo, *Foldats 3690* (NY); lower Ventuari SE of Carmelitas, *Huber 2685* (VEN); San Carlos, *Huber 5676* (NY); 9 km NE of San Carlos de Río Negro, *Liesner 3912* (LL, MO) and *Liesner 3914* (MO); 10 km NE of San Carlos de Río Negro, *Liesner 6925* (LL, MO), *Liesner 7034* (MO); Cerro Sipapo, *Maguire & Politi 28035* (F, NY, VEN); Río Guainía, along Pimichín–Yavita trail near Pimichín, *Maguire et al. 41793* (F, NY); between Esmeralda savanna and SE base of Cerro Duida, *Steyermark 57814* (F, NY); N of Cerro Vinilla, 30 km SSW of Ocamo, *Steyermark et al. 130347 p.p.* (F, LL); Esmeralda, *Tate 300* (NY). BRAZIL. AMAZONAS: Rio Negro, Rio Uneiuxi, 5 km above mouth, *Prance et al. 16213* (NY); Serra Aracá, 0–3 km S of Central Massif, 3 km E of Rio Jauari, *Prance et al. 28861* (MO); Serra Aracá, 1,200 m, *Prance et al. 28978 p.p.* (NY).

This minuscule species of sand savannas resembles in habit members of the difficult *Syngonanthus gracilis* complex and has been found in herbaria under various names, including *S. gracilis* var. *tenuissimus* Ruhl., *S. gracilis* var. *hirtellus* (Steudel) Ruhl., *S. densus* var. *pumilus* Mold., and *S. simplex* (Miq.) Ruhl. It differs from these species in its truly filiform leaves and its generally smaller heads. In addition, the staminate flowers are virtually actinomorphic rather than falcate-asymmetric, and the corollas are fleshy and bulbous, as is sometimes found in the perhaps related species *S. tenuis*. The thickened acuminate apices of the outer involucral bracts also are useful in identification.

Syngonanthus spongiosus Hensold, nom. et stat. nov. *Syngonanthus aquaticus* var. *caespitosus* Mold., Phytologia 24: 19. 1972. TYPE: Brazil. Amazonas: Rio Ituxi, Rio Puciari, Fortaleza Savanna, *Prance et al. 13778* (holotype, LL; isotype, MO).

Because this variety was described with only a very brief diagnosis, a full description is given here. A *nomen novum* is chosen because of prior publication of *Syngonanthus caespitosus* (Wikstr.) Ruhl.

Plants emergent aquatics, with floating leaves and stems producing erect fertile branches bearing umbels at the apex. Stems to 6 cm long, whitish, with a spongy, aerenchymatous cortex, tomentose but early glabrate, densely leafy especially at apex, and producing adventitious roots along the entire length, the roots also white and spongy. Leaves filiform, 1–3 cm long, 0.2–0.3 mm wide, subterete near base, tapered to a blunt apex, glabrous, inconspicuously fenestrate, with a single vein prominent on the lower surface. Fertile branches 1–4 cm long, solitary, naked, deep red-brown or black, sparingly arachnoid-tomentose, bearing a whorl of involucral leaves at the apex, these ca. 5–7 mm long. Inflorescences 3–25 per umbel. Peduncle sheaths 1–2 cm long, lax, obtuse at apex, glabrous or sometimes minutely ciliate around the opening. Peduncles 2.5–9.5 cm long, of differing lengths in the same cluster, 3-costate, glabrous. Capitula 3–4 mm diam. Involucral bracts in 1–2 series, oblong to oblong-obovate, obtuse, hyaline, glabrous, spadiceous, the larger ca. 1 mm long and 0.5 mm wide, well-surpassed by flowers. Receptacle densely lanuginose, the hairs protruding from between the bract bases. Floral bracts present, linear, acute, only about half-equaling the flowers or less. *Staminate flowers.* Pedicels fleshy, 0.4–0.5 mm long. Sepals 3, ca. 1.0–1.1 mm long, the lower 0.3–0.4 mm connate-tubular, the distal portions broadly ovate-elliptic, obtuse, yellowish to spadiceous, glabrous. Corolla tube borne on a fleshy obconic androphore; androphore ca. 0.4 mm long; corolla tube deeply three-lobed, infundibular, membranous, ca. 0.4 mm long, the lobes involute after anthesis. Stamens with filaments exsert; anthers white. Pistillodes present, inconspicuous, whitish. *Pistillate flowers.* Pedicels ca. 0.1 mm long. Sepals 3, free, elliptic to ovate-elliptic, acute, navicular-concave, 1.4–2.0 mm long, yellowish, glabrous or minutely ciliate. Petals linear-subspatulate, subacute, connate at the apex and tightly enclosing the styles, 1.1–1.4 mm long, glabrous. Style 0.1–0.2 mm long; appendages narrowly infundibular, ca. 0.3–0.4 mm long, papillose, the papillae white; style branches simple, ca. 0.7–0.9 mm long, about equaling the petals. Seeds longitudinally striate.

Additional specimens examined. VENEZUELA. APURE: Pedro Camejo, 9 km N of Caño Cochina de La Pica, 80 m, *Davidse & Gonzalez 15994* (LL, MO).

Although not described by its collectors as an aquatic, the stems of *Syngonanthus spongiosus* are evidently submersed or floating, buoyed by the aerenchymatous cortex. Other unusual characters of the species are the densely lanuginose receptacle and the fleshy pedicel and androphore in the staminate flower. It does not bear close affinity to any other Guayanan species.

It is also evidently not closely related to *S. aquaticus* Silveira of the Serra do Cipó, Minas Gerais, Brazil, of which it was described as a variety, in spite of sharing the aquatic habit and filiform leaves. It differs in its conspicuously elongate aerenchymatous stem, its oblong, obtuse, spadiceous involucral bracts, the presence of floral bracts, and a number of floral characters.

Syngonanthus tenuis (HBK) Ruhl., Pflanzenr. IV, 30(13): 253. 1903. *Eriocaulon tenue* HBK, Nov. Gen. Sp. I: 253. 1815. *Paepalanthus tenuis* (HBK) Kunth, Enum. Pl. 3: 282. 1855. *Dupatya tenuis* (HBK) Kuntze, Revis. Gen. Pl. 2: 746. 1891. TYPE: Venezuela. Amazonas: Yavita, banks of Río Tuamini (holotype, B not seen; F photo neg. # 10703).

Syngonanthus drouetii var. *parviceps* Mold., Phytologia 54: 68. 1983. TYPE: Venezuela. Amazonas: N edge of Maroa, *W. W. Thomas 2638* (holotype, LL not seen). Syn. nov.

Syngonanthus tenuis, with its long, white, showy bracts, might be easily mistaken for a member of sect. *Eulepis* Ruhl. Ruhland (1903) recognized on the basis of floral structure that it was more properly placed in sect. *Dimorphocaulon* Ruhl. It is probably not distant from the "*S. gracilis* complex." *Syngonanthus bulbifer*, mistakenly placed by Ruhland in sect. *Eulepis*, is here treated as an imperfectly delimited variety of *S. tenuis*.

The varieties are roughly sympatric, but only occasionally collected at the same site. Variety *tenuis* is characterized by a smaller and more delicate habit than var. *bulbifer*, and unlike var. *bulbifer* does not seem to occur south of Venezuela. Given the high frequency of hybridization in the *Syngonanthus gracilis* alliance, it seems possible

that var. *tenuis* may be the result of gene exchange between var. *bulbifer* and some smaller member of that alliance native to the Amazonian savannas.

The two varieties are keyed as follows.

1a. Leaves 1.2–5.0 cm long, 0.5–2.0 mm wide. Peduncle sheaths 1.6–3.8 cm long. Peduncles 10–27.5 cm long, ca. 1–15 per rosette. Disc of capitulum 4–5.5 mm diam., the upper bracts waxy white, oblanceolate-rounded, often held erect or slightly radiating in dry material. Flowers ca. 1.4–1.8 mm long ..... *Syngonanthus tenuis* var. *bulbifer*

1b. Leaves 0.4–3.8 cm long, 0.2–1.0 mm wide. Peduncle sheaths 0.8–2.0(–3.0) cm long. Peduncles 4–14 cm long, ca. (4–)8–60 per rosette. Disc of capitulum 2.5–4(–4.5) mm diam., the upper bracts hyaline or with waxy white streaks, obovate to broadly oblanceolate, always cupped over the disc in dry material. Flowers ca. 1(–1.4) mm long ..... *Syngonanthus tenuis* var. *tenuis*

Syngonanthus tenuis var. **bulbifer** (Huber) Hensold, comb. et stat. nov. *Paepalanthus bulbifer* Huber, Bol. Mus. Paraense Hist. Nat. 2: 499. 1898. *Syngonanthus bulbifer* (Huber) Ruhl., Pflanzenr. IV. 30: 272. 1903. TYPE: Brazil. Amapá(?): Rio Maracá, *Guedes in hb. Amaz. Mus. Paraens., no. 601* (holotype, MG not seen; isotype, B not seen, F photo neg. # 10676).

Syngonanthus drouetii Lyman B. Smith, Contrib. Gray Herb. 117: 34, pl. 2, figs. 41–43. 1937. TYPE: Brazil. Pará: 4 km S of Vigia, *Drouet 2112* (holotype, GH not seen; isotype, F). Syn. nov.

Syngonanthus vaupesanus Mold., Phytologia 2: 6. 1941. TYPE: Colombia. Vaupés: Yurupari, ca. 350 km above Mitú, *Cuatrecasas 6973* (holotype, US). Syn. nov.

Syngonanthus vareschii Mold., Acta Biol. Venez. 2(7): 50. 1957. TYPE: Venezuela. Bolívar: Auyán-tepui, Guayaraca, 1,100 m, *Vareschi & Foldats 4576* (holotype, VEN not seen; isotypes, LL, NY).

This species is based on a mixed collection. The vegetative portion included in the isotype material I have seen and also unmistakably portrayed in the original description is the moss *Octoblepharum pulvinatum* (Dozy & Molk.) Mitt. (det. Bruce Allen). The inflorescences appear to be those of depauperate material of *Syngonanthus simplex* (Miq.) Ruhl., which is common in the Gran Sabana.

Syngonanthus williamsii (Mold.) Hensold, comb. nov. *Paepalanthus williamsii* Mold., Phytologia 2: 367. 1947. TYPE: Venezuela. Amazonas: Upper Orinoco, San Antonio, *Williams 15051* (holotype, NY; isotype, F).

This species is a good *Syngonanthus*, possessing all the essential characters of that genus, i.e., petals of the pistillate flowers connate medially, trichomes of the inflorescence smooth and acute, roots white and spongy. Its habit and floral structure indicate close affinities to *S. longipes* Gleason and *S. appressus* (Koern.) Ruhl.

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REVISION AND REDEFINITION OF THE GENUS *RONDONANTHUS* HERZOG (ERIOCAULACEAE)[1]

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Ana Maria Giulietti[3]

ABSTRACT

The genus *Rondonanthus* Herzog has until now contained only the species *R. roraimae* and *R. micropetalus*, and has been defined by free petals in both sexes of flowers and the dioecious condition. It is here redefined according to a large suite of characters, especially the presence of long filamentous staminodes in the pistillate flowers, and by the adnation of the filament base to the corolla in the staminate flowers. Five additional species, including the monotypic genus *Wurdackia*, are transferred to *Rondonanthus*, and *R. micropetalus* is removed to *Paepalanthus*. It is proposed that *Rondonanthus* is a highly primitive paepalanthoid genus, to be taken as a primitive outgroup of *Syngonanthus*.

The Eriocaulaceae are a pantropical monocot family of about 13 genera and 1,200 species (Kral, 1989). Except in rare cases, the flowers are unisexual and the plants monoecious, with the flowers borne in scapose heads.

Ruhland (1903) divided the family into two subfamilies, the Eriocauloideae, characterized by two whorls of stamens and a simple gynoecium, and the Paepalanthoideae, with a single whorl of stamens and vascularized secretory "appendages" inserted on the style alternate with the nonvascularized functional style branches. The Eriocauloideae are truly pantropical and contain many aquatic species, while the Paepalanthoideae are almost entirely limited to the New World (with some African disjuncts), and more xerophytic.

The Paepalanthoideae, which contain 11 of the 13 genera, have two centers of diversity, one in the Central Brazilian Plateau, especially the Cadeia do Espinhaço in Minas Gerais and Bahia, and one in the Guayana Highland, especially Venezuela. Botanical exploration of Guayana, in particular the tepui summits of Venezuela, has only been undertaken recently relative to that of the more accessible mountains of central Brazil, and has turned up many taxa of interest, including four endemic paepalanthoid genera. These are *Rondonanthus* Herzog (1931), *Comanthera* Lyman B. Smith (1937), *Carptotepala* Mold. (1951), and *Wurdackia* Mold. (1957).

Following the lead of Ruhland (1903), all of these genera were described with reference to only a few floral characters. None contain more than two species, and none were discussed by their authors as to their relationships with other genera or implications for phylogeny. Recently, the availability of abundant collections from the Venezuelan tepuis and their study for Julian Steyermark's *Flora of the Venezuelan Guayana* (Hensold, in prep.) have acutely emphasized the need for study and reevaluation of these endemic genera.

In another work (Giulietti & Hensold, 1991), we discuss the systematic position of *Comanthera* and *Carptotepala*, concluding that they are synonyms of *Syngonanthus* Ruhl. In this work, we find the genus *Rondonanthus* to be valid, though in need of redefinition, and include within it five additional endemic Guayanan species currently placed in three other genera, including the monotypic genus *Wurdackia*.

Rondonanthus as here recognized is a genus of great interest from the standpoint of phylogeny in

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Eriocaulaceae. It appears to combine characters of the Eriocauloideae with characters of two "core" paepalanthoid genera, *Paepalanthus* and *Syngonanthus*. As Stützel (1985) concluded (limiting his observations to *R.* (*Wurdackia*) *flabelliformis*), it appears to represent a primitive outgroup to the large genus *Syngonanthus*. As a genus, it also shows unusual variability with respect to certain floral characters, such as fusion of perianth parts and flower sexuality, which have until now been given a priori value in the definition of genera of Eriocaulaceae.

Taxonomic History

The genus *Rondonanthus* was described by Herzog (1931) on the basis of a single Luetzelburg collection of *R. roraimae* (Oliver) Herzog, based on *Paepalanthus roraimae* Oliver.

Herzog found only staminate flowers in his material and defined the genus by the free petals of the male corolla, which he believed to be unknown in *Paepalanthus*. Because he did not see the type material, he depended on Oliver's illustrations for his description of the pistillate flowers, which he described correctly as having the petals free and incorrectly as having simple style branches. Herzog also noted that the limited material he studied was dioecious and suggested this as an additional character of the genus, also encountered rarely in the family.

Ruhland (1903), in his comprehensive treatment of the family, had in fact erected *Paepalanthus* subg. *Bostrychophyllum* Ruhl. to accommodate *P. capillaceus* Klotzsch ex Koern., the single known species of *Paepalanthus* with free petals in the staminate flowers. This species is a vegetatively specialized submerged aquatic also native to Roraima, and is here treated as a species of *Rondonanthus*. (Ruhland had placed *P. roraimae* in "Species dubiae" since he had observed no material of the species.)

The same year that Herzog described *Rondonanthus*, Gleason (1931) described *Paepalanthus duidae* from Cerro Duida in Amazonas, noting the close similarity to *P. roraimae* Oliver, and differentiating it from that species only by minor characters of gross morphology, and without mention of floral structure.

Later, additional species of *Rondonanthus* were described from the Chimantá Massif and placed in *Syngonanthus* (*S. acopanensis* Mold., 1948, and *S. obtusifolius* Mold., 1957), and in a new monotypic genus *Wurdackia* (*W. flabelliformis* Mold., 1957). All exhibit typical *Syngonanthus*-like corollas, with the corollas of the staminate flowers tubular and those of the pistillate flowers connate at the middle and free at the base and the apex. *Wurdackia*, however, differed in being the first known species of the family with bisexual flowers.

All of these taxa are here treated in *Rondonanthus*, though their differences in corolla fusion characteristics and flower sexuality originally caused them to be assigned to four different genera.

The only other species described in *Rondonanthus* since the type species, *R. micropetalus* Mold. (1951), reputedly with free petals in the staminate flowers, is here removed to synonymy in *Paepalanthus* Ruhl. (see Excluded Species).

Generic Definition and Affinities

The single character that best distinguishes *Rondonanthus* from all other genera of Eriocaulaceae is the presence of long linear staminodes in the pistillate flowers. Staminodes are known in *Paepalanthus*, but they are small and scalelike, never linear. The only species of *Rondonanthus* in which these are not found is *R. flabelliformis*, in which they are replaced by functional stamens which produce and release pollen in apparently normal quantities.

Rondonanthus is further defined by a mixture of characters individually found in other genera, especially *Syngonanthus* and *Paepalanthus*, but not in combination with each other.

The affinities of *Rondonanthus* appear to lie most closely with *Syngonanthus*, for a number of reasons. In *R. acopanensis*, *R. caulescens*, and *R. flabelliformis*, the petals of the pistillate flowers are fused in the middle but free at the base and apex, which is considered to be one of the defining characters of *Syngonanthus*. Elsewhere in the Eriocaulaceae, this is known only in the genus *Philodice* C. Martius (2 spp.), which is considered to be derived from *Syngonanthus*, and in *Mesanthemum* Koern., which with two whorls of stamens and an unmodified gynoecium is quite distant from *Rondonanthus*.

This character, however, is not stable in the genus. In *R. roraimae* and *R. capillaceus*, the petals of the pistillate flowers are always free, and in the variable species *R. duidae*, most populations have free petals, but a single population has been found (at Aprada-tepui) with brief petal fusion. In the genus *Syngonanthus*, the character also shows a small degree of instability. In the reduced, dimerous species *S. minutus* (Mold.) Hensold (1991), for example, the petals are free, and this situation is also occasionally found in sect. *Thysanocephalus*

(Koern.) Ruhl., as in *S. jenmanii* (Gleason) Giulietti & Hensold (1991). Petal fusion probably represents a primitive state in *Rondonanthus*, as is also considered to be the case in *Syngonanthus*.

Fusion of the corollas of the staminate flowers is a fairly universal condition in the Paepalanthoideae, but this character also breaks down in *Rondonanthus*. Of the species with free petals in the pistillate flowers, *R. capillaceus* also has free petals in the staminate flowers, *R. roraimae* has petals connate early in development and then separating, and *R. duidae*, except in very rare cases, has petals persistently connate. The remaining three species, which all exhibit fusion of corollas in the pistillate flowers, similarly have fused corollas of the staminate flowers.

Other characters which indicate an alliance with *Syngonanthus* are the following: roots pale and aerenchymatous; hairs present on the floral axis at ovary base; base color of the perianth creamy white; pubescence of malpighian hairs on vegetative parts. All of these characters except the last may also be found in the genus *Leiothrix* Ruhl., but this genus is differentiated by specialized morphology of the gynoecium, seed testa striations, and basifixed anthers (Giulietti, 1984).

Stützel (1988) found similar root anatomical structure in *R. roraimae*, *Syngonanthus* (*Carptotepala*) *jenmanii* (sect. *Thysanocephalus*), and *Mesanthemum*. A divergent type of aerenchymatous morphology was observed in *S. chrysanthus* (Bong.) Ruhl. (sect. *Dimorphocaulon* Ruhl.), *S. caulescens* (Poiret) Ruhl. (sect. *Carphocephalus* Ruhl.), and *Philodice*.

Aerenchymatous roots are unknown in the genus *Paepalanthus*, however, and we also have never observed malpighian hairs in this group. The presence of hairs at the base of the ovary is a character that has not been systematically surveyed in the family but which we have not encountered in *Paepalanthus*. The white base color of the perianth and often also the involucral bracts is a conspicuously common character in *Syngonanthus*, but probably rare (if at all present) in *Paepalanthus*.

On the other hand, a number of other characters occur in *Rondonanthus* which are much more commonly observed in *Paepalanthus*. The most notable is the deeply bifid style branches found in all species of *Rondonanthus* and in most *Paepalanthus*, but never described from *Syngonanthus* or *Leiothrix*.

Certain characteristics are shared by *Rondonanthus* with *Paepalanthus* and also the putatively more primitive Eriocauloideae (*Eriocaulon* L. and *Mesanthemum*). These are: the opaque blackish coloration of the involucral bracts, and frequently also the upper parts of the perianth; the tufts of trichomes on the tips of the sepals and floral bracts; the clavate or subclavate shape of these perianth trichomes, which sometimes (*R. capillaceus*) are densely ornamented on the internal wall; and, in three species, the ciliate margins of the staminate flower corollas.

All of these characteristics are common in the Eriocauloideae. The last is not known from any species of *Syngonanthus*, but is common in some of the less specialized members of *Paepalanthus*, notably subg. *Xeractis*. Inner wall ornamentation in floral trichomes has also not been described from *Syngonanthus* but is the rule in *Paepalanthus*. Bearded sepal apices are known in *Syngonanthus* (especially in sect. *Dimorphocaulon*, e.g., *S. humboldtii* (Kunth) Ruhl., *S. diamantinensis* Silveira), but not common, and involucral bract pigmentation, when it occurs, is usually more or less translucent and reddish (*S. arenarius* (Gardner) Ruhl., *S. anomalus* (Koern.) Ruhl.). An exception is *S. niger* Silveira, with long black linear-lanceolate bracts.

Furthermore, in *R. acopanensis*, the outermost bracts, as well as the inner bract apices, are apparently green and leaflike when young, which may be interpreted as a lack of specialization. This same situation is also found in some species of *Paepalanthus* subg. *Xeractis* Koern. (*P. digitiformis* Hensold, *P. dianthoides* Koern.).

Thus, certain parallels can be drawn between *Rondonanthus* and *Paepalanthus* subg. *Xeractis*, which are both interpreted as primitive within their respective lineages (Hensold, 1988). Both possess, in their less specialized species, lanceolate, leaflike bracts which surpass the head. In subg. *Xeractis* these bracts are commonly pubescent on the inner surface, and this is also found occasionally in *Rondonanthus*, as also in *Mesanthemum*. Both also have typically pilose corollas of the staminate flowers, though this is also an extremely rare characteristic elsewhere in the Paepalanthoideae, known only in a few species of *Paepalanthus* closely related to subg. *Xeractis*.

Another exceptional character of *Rondonanthus* is the fusion of the filament base with the corolla. This occurs in four of the five species of *Rondonanthus*. (In *R. capillaceus*, the only species in the genus with an "androphore," or elongated floral axis above the sepals, the petals are inserted at the base of the androphore while the stamens are inserted at its apex, and therefore adnation of the filaments is impossible.) Adnate filaments are common in the Eriocauloideae (both

Eriocaulon and *Mesanthemum*) but not heretofore documented in the Paepalanthoideae. (We have also found them to occur in *Syngonanthus* sect. *Carphocephalus* and in *S. amazonicus* Mold.)

Implications for Phylogeny

Rondonanthus thus combines characteristics of the Eriocauloideae, *Paepalanthus* and *Syngonanthus*. It apparently has strong affinities to *Syngonanthus* but differs from that genus in characters that seem more primitive in the subfamily or family as a whole. Moreover, it presents variation in flower sexuality, fusion of the petals, and presence of trichome wall thickenings, all characters which have been used to define genera.

Stützel (1985), studying *R.* (*Wurdackia*) *flabelliformis*, posited it as an "evolutionary link" between *Syngonanthus* and *Mesanthemum*. *Mesanthemum* also shows *Syngonanthus*-like fusion of the pistillate flower corolla, but like *Eriocaulon* possesses two whorls of stamens and an unmodified gynoecium. As evidence, Stützel cited (a) the bifid style branches of *Wurdackia*, which he interpreted as primitive relative to the simple style branches of *Syngonanthus*; and (b) the adnation of the filaments to the corolla shared by "*Wurdackia*" and *Mesanthemum*, but believed by him to be lacking in *Syngonanthus*.

Stützel did not consider the bisexual flower of "*Wurdackia*" to represent a necessarily primitive state, observing that in eriocauls differentiation of floral sexuality occurs late in development (Stützel, 1985) and might be readily subject to evolutionary modification. Having found that (1) bisexual flowers occur together with staminate flowers in the same head; (2) "*Wurdackia*" has very close sympatric relatives with normal pistillate and staminate flowers; and (3) these related species possess long filamentlike staminodes in the pistillate flowers, we agree that the bisexual flowers of "*Wurdackia*" are probably secondarily derived.

In the same publication, Stützel (1985) proposed a new three-subfamily system of classification for the Eriocaulaceae, in which the Syngonanthoideae (*Mesanthemum*, *Wurdackia*, *Syngonanthus*, and *Philodice*) and the Paepalanthoideae s. str. (*Paepalanthus*, *Lachnocaulon* Kunth, *Tonina* Aublet, *Blastocaulon* Ruhl., and *Rondonanthus*) are independently derived from the Eriocauloideae, containing only *Eriocaulon*.

Rondonanthus (represented only by *R. roraimae*) was evidently placed in the Paepalanthoideae because of the free petals in the pistillate flowers. The union of *Wurdackia* with *Rondonanthus*, however, does not create problems for Stützel's phylogeny, especially if we suppose that free petals are a derived character in the genus. In addition, the styles of *Rondonanthus* s.l. are shown to be bifid, rather than simple, and the filaments adnate to the corolla, all of which characters are compatible with Stützel's system.

This three-subfamily system is problematic, however, not in its phylogenetic interpretation of "*Wurdackia*," but in the cladistic emphasis it places on "syngonanthoid" fusion of the pistillate flower corolla. Stützel cited scanning electron microscope (SEM) developmental studies of flowers (Stützel, 1984) which have revealed the pistillate flower corolla of *Syngonanthus* to be congenitally fused, while that of *Paepalanthus* is shown to be congenitally free. He concluded that the flowers of *Paepalanthus* cannot be derived phylogenetically from those of *Syngonanthus*, and that the genus must therefore have a separate origin in the Eriocauloideae, perhaps in *Eriocaulon*, in which petals of both sexes of flowers are free.

This classification, however, assumes that evolution of the highly modified gynoecium with its "stylar appendages," not to mention the reduction of stamens from two whorls to one, must occur twice in evolution. The alternative is to assume either that (a) the syngonanthoid corolla arose twice in separate lines, or (b) *Paepalanthus* was originally derived from a species with a syngonanthoid corolla, in spite of the lack of ontogenetic evidence.

The first alternative does not seem unlikely, especially in view of the finding that corolla fusion is a character showing much less stability, especially in the primitive genus *Rondonanthus*, than that of gynoecial modification. The paepalanthoid gynoecium furthermore must be thought of as involving more than one major evolutionary change, i.e., the modification of the ancestral style into an "appendage" (nectary) and the formation of nonvascularized functional styles at a position rotated 60 degrees from the position of the original styles. As far as we know there are no intermediate forms in existence, and no cases in the Paepalanthoideae where the gynoecium has reverted to the primitive state. The second alternative is also not hard to visualize, if we do not assume that ontogeny faultlessly recapitulates phylogeny.

We agree that *Syngonanthus* and its allies seem to constitute a natural group which may be usefully distinguished from *Paepalanthus* and its allies. What is most necessary at present is to survey the subgenera and sections of these two large, polymorphous, and probably unnatural genera in an effort to better characterize the taxa involved and

to more fully identify and survey characters of evident taxonomic importance.

Moreover, if *Rondonanthus* is taken as a primitive outgroup of *Syngonanthus*, it may aid in the assessment of whether *Syngonanthus* is mono- or polyphyletic, and if the latter, how it is to be properly divided to reflect phylogeny.

We feel it is more practical and parsimonious to retain for the present Ruhland's two-subfamily classification while acknowledging that much more information is needed to build a strong phylogenetic understanding of Eriocaulaceae.

Taxonomy

Rondonanthus Herzog, Feddes Repert. Spec. Nov. Regni Veg. 29: 210. 1931. TYPE: *Rondonanthus roraimae* (Oliver) Herzog.

Wurdackia Mold., Mem. New York Bot. Gard. 9: 413. 1957. TYPE: *Wurdackia flabelliformis* Mold.

Paepalanthus subg. *Bostrychophyllum* Ruhl., Pflanzenr. IV. 30: 220. 1903. TYPE: *Paepalanthus capillaceus* Klotzsch ex Koern.

Plants rosulate or caulescent cespitose perennials branching at ground level. Roots creamy white to pale brown, porous (aerenchymatous), brittle, not spongy, usually sparingly branched, the branches evidently much smaller in diameter than main roots. Stems ca. 2–10 mm diam., woolly with fine cream to tan-colored filamentous hairs. Leaves spirally arranged or distichous, filiform to linear or ligulate, the young leaves attaining full width long before full length; the bases also with parallel margins, but dilated with respect to the blades, at least distally, somewhat scarious and frequently woolly with hairs like those of the stem. Pubescence of leaves and peduncles when present mostly a mixture of filamentous and malpighian hairs, the latter usually "retrorse" (i.e., strongly asymmetric with the larger end proximal); capitate hairs lacking. Inflorescences single to numerous per age class and then usually ± synchronous. Peduncle sheaths ± membranous with respect to the leaves, often pale and scarious at least toward the upper margin, closed over the young inflorescences and splitting down one side from just below the apex, the opening oblique with the upper margins remaining minutely involute and often eventually lacerate. Peduncles mostly 3- or 6-costate, sometimes apparently more. Capitula turbinate to hemispheric at maturity, rarely subglobose. Involucral bracts, or at least their visible apices, triangular to lanceolate, acute to subacute, gold to nearly black, or variegated. Receptacle pilose. Floral bracts present, usually about equaling the flowers, linear to spatulate, pubescent abaxially at apex. Flowers 3-merous, either staminate and pistillate or staminate and bisexual, the two types usually found in different zones in the same capitulum or rarely (*R. roraimae*) most capitula and plants unisexual. *Staminate flowers.* Pedicels 0.3–2.5 mm, sometimes equaling or even exceeding the flowers in length. Sepals free, elliptic to spatulate, pubescent abaxially at apex. Petals free or connate into a 3-lobed tube, and then sometimes separating after anthesis, glabrous or pilose at upper margin. Androphore usually lacking; when present, the petals free and borne at its base. Stamens adnate to corolla at base, except when separated from corolla by androphore; anthers dorsifixed, white or cream. *Pistillate and bisexual flowers.* Pedicels 0.2–2.0 mm long. Sepals free, ovate to elliptic to spatulate, pigmented as in the staminate flowers or lighter, pubescent as in the staminate flowers, expanding and thickening with maturation of the fruit, especially at base. Petals free or connate distally and free at the base, glabrous or pilose at upper margin and abaxially. Linear staminodes, or more rarely fully developed stamens, present opposite petals, the staminodes usually about half to twice the height of the ovary and bearing two tiny brownish lobes at the apex. Ovary usually subtended by a ring of long hairs, the style much shorter than the style branches; the appendages infundibular, stalked, papillose, inserted on style at or commonly slightly below the level of divergence of the style branches; the style branches strongly bifid. Fruit a loculicidal capsule. Seeds ellipsoidal, reticulate, the longitudinal striations of the testa raised and more conspicuous than the transverse. Floral trichomes subacute to subclavate, with or without granular thickenings of the internal wall.

Key to the Species of *Rondonanthus*

1a. Plants submerged aquatics; leaves filiform-setaceous, usually surpassing the peduncles; heads 3–5 mm diam.; floral bracts and sepals short-hairy ..... *R. capillaceus*

1b. Plants terrestrial; leaves linear to ligulate, always surpassed by peduncles; heads 6–19 mm diam.; floral bracts and sepals densely bearded with long hairs.

2a. Leaves distichous.

3a. Stems leafy to base; flowers bisexual and staminate ..... *R. flabelliformis*

3b. Stems leafy only at apex; flowers pistillate and staminate ..... *R. acopanensis*

2b. Leaves spirally arranged.

4a. Peduncles 3-costate; involucral bracts of upper series acuminate, the acumen colorless ..... *R. caulescens*

4b. Peduncles 6-costate; involucral bracts of upper series subacute to acute, black

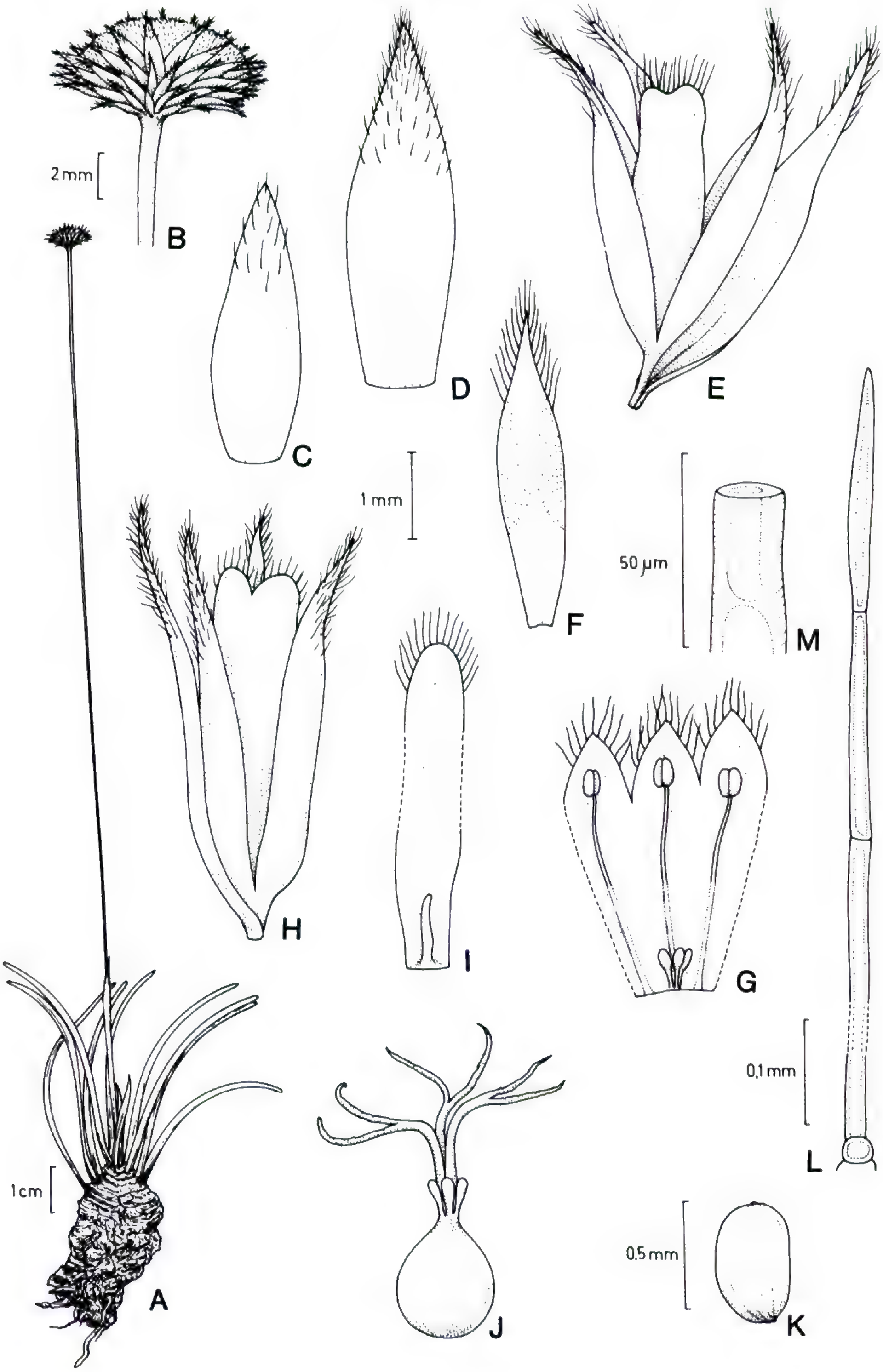


FIGURE 1. *Rondonanthus acopanensis* (Mold.) Hensold & Giulietti var. *acopanensis* (*Steyermark 128872* MO).—A. Habit.—B. Inflorescence.—C, D. Involucral bracts. E–G. Staminate flower.—E. Flower with bract, past anthesis (corolla involute at upper margin).—F. Sepal, adaxial view.—G. Corolla tube, opened to show stamens and pistillodes. H, I. Pistillate flower.—H. Flower with bract, past anthesis.—I. Petal, with hatched lines showing where fused with adjacent petal, and staminode adhering at base.—J. Gynoecium (fruiting).—K. Seed.—L, M. Trichome of floral bract apex.

at apex and margins, though sometimes the midvein pale.

5a. Leaves sharp-cuspidate to aristate; petals of staminate flowers persistently connate and ciliate at upper margin ..... *R. duidae*

5b. Leaves obtuse to subacute; petals of staminate flowers connate early but separating by anthesis, glabrous ..... *R. roraimae*

Rondonanthus acopanensis (Mold.) Hensold & Giulietti, comb. nov. *Syngonanthus acopanensis* Mold., Phytologia 3: 41. 1948. TYPE: Venezuela. Bolívar: Chimantá Massif, Cerro Acopán, 1,900 m, *Cardona 2280* (holotype, US; isotype, NY). Figure 1.

Plants short-stemmed cespitose perennials. Main roots ca. 0.5–1.2 mm diam., sparingly branched, cream to pale orange-brown. Stems 1–4 cm long at flowering, ca. 2–5 mm diam., leafy only near apex, but the lower portions covered with tightly persistent flabelliform leaf bases (these making the stem appear laterally compressed and 5–20 mm wide), woolly with cream-colored hairs. Leaves distichous, 3–13 cm long, 1–4(–6) mm wide, the base and blade abruptly differentiated, the base linear, dilated with respect to blade, scarious, densely enfolded with long cream-colored woolly hairs (often black with dirt), and persistent, a transverse abscission layer apparently forming at the juncture with the blade; the blades linear, subacute to broadly rounded or truncate depending on width, cartilaginous and rigid, glabrous or pubescent with retrorse malpighian hairs when young especially adaxially, 5–30-veined, the veins of equal size. Inflorescences single per age class, the old ones often persistent on stem. Peduncle sheaths 2–11 cm long, twisted, mostly striate-pubescent with retrorse malpighian hairs, the apex acute to rounded (corresponding in shape to leaf apex), green or scarious, frequently lacerate with age. Peduncles 12–45(–60) cm long, 6-costate, sometimes apparently more by division, pubescent with retrorse malpighian hairs and long filamentous hairs fringing the base of the capitulum. Capitula 7.5–12(–15) mm diam., turbinate to hemispheric at maturity. Involucral bracts in 3–5 series, the outer narrowly triangular to lance-linear, subacute to acute, erect to slightly recurved-spreading, 2.5–5.5 mm long, 0.6–1.0 mm wide at base, the inner bracts oblanceolate, broadly acuminate, erect, 4–7 mm long, 0.8–1.3 mm wide, mostly surpassing the head by ca. 0.5–1.5 mm; the outer bracts pale brown to castaneous, or greenish when fresh, the inner black except for the pale tip and midvein; the outer bracts usually ciliate and hirsute abaxially, the inner densely bearded at the apex, at least abaxially and sometimes also adaxially, glabrate with age. Floral bracts commonly exceeding the flowers, linear to linear-oblanceolate, acuminate, sometimes with a long "whip tip," blackened distally, tufted with hairs abaxially at apex. *Staminate flowers.* Pedicels 0.7–1.3 mm long. Sepals obovate-elliptic to spatulate, attenuate-acute to long-acuminate, 2.3–3.5(–4.0) mm long, 0.6–0.9 mm wide, white at base, blackened distally except for white midvein and apex, the apex tufted abaxially with divergent trichomes like a bottlebrush. Corolla connate into a 3-lobed tube, the androphore lacking, the tube 2.0–3.5(–4.5) mm long, the lobes triangular-obtuse, the upper margin and abaxial lobe apices ciliate-pilose, involute and retracting the stamens after anthesis. Stamens with filaments adnate to corolla at base, ± included; anthers ca. 0.3–0.35 mm long. *Pistillate flowers.* Pedicels 0.6–0.8 mm long. Sepals elliptic to ovate-elliptic, concave, acuminate, 3.5–4.0(–4.7) mm long, 1.0–1.5 mm wide, cream-colored or pigmented as in staminate flowers though usually more weakly so, tufted at the apex as in the staminate flowers, thickening at base at maturity. Petals connate into a tube except at base, the segments oblong, ± rounded at apex, 2.8–3.5(–4.7) mm long, 0.6–0.9 mm wide, densely ciliate at upper margin and frequently also pilose abaxially at apex or in submarginal bands. Staminodes linear, 0.6–1.3(–2.5) mm long. Ovary ringed by hairs at base, 0.4–0.7 mm long, the style 0–0.3 mm long, the appendages ca. 0.4 mm long, the stalk thick, the papillose portion orange-brown, the style branches diverging slightly above the appendages, 1.5–2.3 mm long, conspicuously bifid. Floral trichomes subacute to rounded, lacking granular thickenings of the internal wall.

This species is endemic to the Chimantá Massif in Bolívar, Venezuela, where it is represented by two sympatric varieties, heretofore recognized as species. They are about equally commonly collected and are distinguishable only by their size and robustness, as well as possible habitat differences. This sort of variation crops up not uncommonly in eriocauls (as in *Paepalanthus superbus* Ruhl. and *P. chlorocephalus* Silveira in the Serra do Cipó, Brazil; Hensold, 1988), and is possibly associated with polyploidy or some other macromutation. This would imply that the larger form may be "polyphyletic," having been derived several times from the smaller form. (An alternative view would be that the smaller form may have been derived from the larger form.) However, because we lack cytological data, and since each type is

about equally widespread and forming uniform populations, we have treated them as varieties.

1a. Leaves 1–2 mm wide; heads 7.5–10 mm diam.; involucral bracts mostly ca. 3-seriate ..... *Rondonanthus acopanensis* var. *acopanensis*

1b. Leaves (2–)2.8–6 mm wide; heads 10–14(–15) mm diam.; involucral bracts mostly ca. 4–5-seriate ..... *Rondonanthus acopanensis* var. *obtusifolius*

Rondonanthus acopanensis var. **acopanensis**

Stems, including attached leaf bases, ca. 5–10 mm wide. Leaves 1–2 mm wide, 5–7(–9)-nerved, firm, green, subacute, the margins not turning shiny brown. Heads 7.5–10 mm diam. Involucral bracts in 3 series, the lowest lanceolate, 2.5–3.5 mm long, 0.6–0.9 mm wide. Floral bracts 3.5–4.7 mm long. Staminate flowers with sepals 2.3–3.3 mm long, 0.6–0.8 mm wide, and corollas 2.0–2.7 mm long. Pistillate flowers with sepals 3.5–4.0 mm long, 1.0–1.4 mm wide, and corollas 2.8–3.2 mm long.

Phenology. Collected in flower mostly from January to March, but also occasionally in June and August.

Habitat and distribution. Locally abundant on wet sandy depressions and banks on shallow soils, in the open or in scrub forest, 1,900–2,600 m. Venezuela. Bolívar: Chimantá Massif (Acopán-, Apácara-, Chimantá-, Murey- (Eruoda-)tepuis).

Additional specimens examined. VENEZUELA. BOLÍVAR: Chimantá Massif, Apácara-tepui, N section, *Huber & Colella 8685* (LL, NY, VEN), *Huber & Colella 8737* (LL, NY); Apácara-tepui, E-central section, *Steyermark 75925* (F); Apácara-tepui, S section, *Huber & Steyermark 6964* (LL, MO), *Huber & Steyermark 6970* (LL); Apácara-tepui, SE section, *Steyermark 75850* (F); Chimantá Massif, Murey- (Eruoda-)tepui, *Huber 11575* (NY), *Steyermark 115818-A* (LL, VEN); Chimantá Massif, Chimantá-tepui, central-NE sector, *Steyermark et al. 128165* (LL, MO, NY, VEN); Chimantá-tepui, E sector, vicinity of Caño del Grillo, *Huber & Steyermark 7160* (LL, MO), *Steyermark & Wurdack 804* (F, NY), *Steyermark 128872* (LL, MO), *Steyermark 128938* (LL); Chimantá Massif, Churi-tepui, *Wurdack 3421*3 (F, NY, VEN), central-SE section, *Huber & Colella 8934* (LL, NY), *Huber 9275* (MO); Angasima-tepui, 10 km SE of Chimantá Massif, *Huber 11688* (MO).

Rondonanthus acopanensis var. **obtusifolius** (Mold.) Hensold & Giulietti, comb. et stat. nov. *Syngonanthus obtusifolius* Mold., Mem. New York Bot. Gard. 9: 410. 1957. TYPE: Venezuela. Bolívar: Chimantá Massif, central section, 1,940 m, 4 Feb. 1955, *Steyermark & Wurdack 406* (holotype, NY; isotypes, F, GH).

Stems, including attached leaf bases, ca. 12–20 mm wide. Leaves (2–)2.8–6 mm wide, ca. 11–19(–30)-nerved, rounded to nearly truncate, very firm-coriaceous (only firmly chartaceous in *Huber 11522*), the margins, especially near the apex, often shiny and deep brown-tinged. Heads 10–14(–15) mm diam. Involucral bracts in (3–)4–5 series, the lowest lance-linear, ca. 3.5–6 mm long, 0.7–1.0 mm wide. Floral bracts 3.5–6.2 mm long. Male flowers with sepals 3.0–3.5(–4.0) mm long, 0.6–0.9 mm wide, corolla 3.0–3.5(–4.5) mm long. Female flowers with sepals ca. 3.5(–4.7) mm long, ca. 1.3–1.5 mm wide, corolla 3.0–3.5(–4.7) mm long.

Phenology. Collected in flower late January to mid-March.

Habitat and distribution. Locally abundant in open wet savanna and among sandstone outcrops, at 1,800–2,200 m. Venezuela. Bolívar: Chimantá Massif (Abacapá-, Acopán-, Apácara-, and Chimantá-tepuis).

Additional specimens examined. VENEZUELA. BOLÍVAR: Chimantá Massif, Apácara-tepui, S sector, *Huber & Steyermark 7061* (LL, NY), *Steyermark 128428* (LL, MO), *Steyermark et al. 128519* (LL, MO); Apácara-tepui, SE sector, *Huber et al. 8854* (LL, NY), *Huber et al. 8878* (LL, NY), *Huber 11522* (MO), *Huber 11524* (NY); Chimantá-tepui, NE sector, *Huber & Steyermark 6864* (LL, NY); Chimantá-tepui, central-NE sector, *Steyermark et al. 128090* (NY, MO); Chimantá-tepui, central-S sector, *Huber et al. 10179* (MO); Abacapá-tepui, S sector, *Huber & Dezzeo 8620* (NY); Acopán-tepui, W sector (Amurí-tepui), *Huber & Steyermark 7082* (LL, VEN), *Steyermark et al. 128453* (LL, MO), *Steyermark et al. 128793* (LL); Acopán-tepui, NE sector, *Huber et al. 10152* (NY), SE sector, *Huber 9065* (LL, NY), SSE sector, *Steyermark et al. 129909* (LL, VEN).

The specimen *Huber 11522* is included here with some reservation. It differs from typical var. *obtusifolius* not only in its overall larger dimensions, but in lacking stem elongation, a distichous leaf arrangement, and coriaceous-thickened leaves. Normal var. *obtusifolius* (*Huber 11524*) has been collected from the same locality.

Rondonanthus capillaceus (Klotzsch ex Koern.) Hensold & Giulietti, comb. nov. *Paepalanthus capillaceus* Klotzsch ex Koern. in C. Martius, Fl. Bras. 3(1): 415, t. 53, fig. II. 1863. *Dupatya capillacea* (Klotzsch ex Koern.) Kuntze, Revis. Gen. Pl. 2: 745. 1891. TYPE: Guyana: savannas of Mount Roraima and Humiridia, April–May, *Schomburgk 1222* (holotype, B not seen). Figure 2.

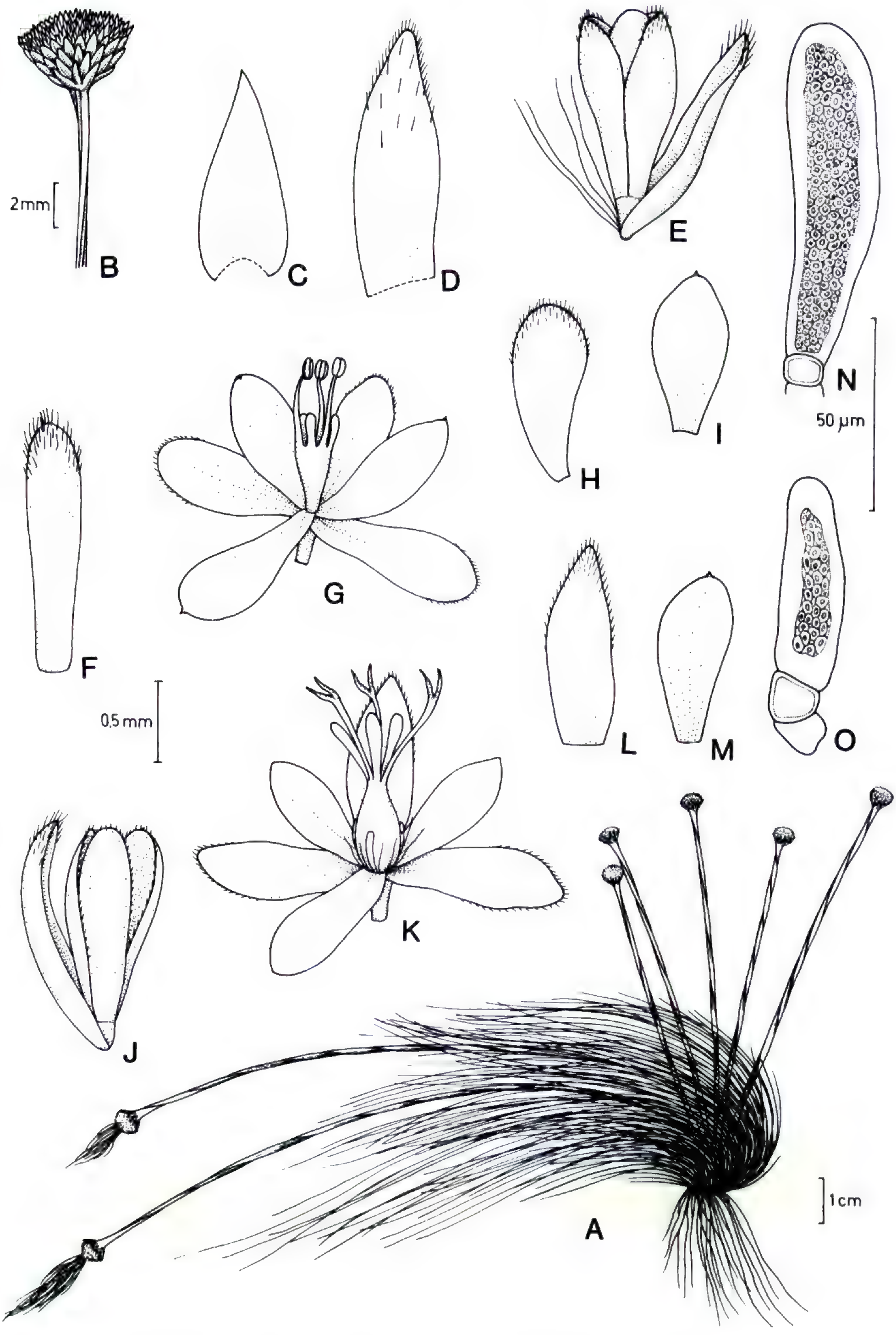


FIGURE 2. *Rondonanthus capillaceus* (Klotzsch ex Koern.) Hensold & Giulietti (*R. Kral 72131* MO).—A. Habit.—B. Inflorescence.—C, D. Involucral bracts, lower and upper. E–I. Staminate flower.—E. Whole flower, with floral bract.—F. Floral bract.—G. Flower with perianth spread open.—H. Sepal, abaxial view.—I. Petal. J–M. Pistillate flower.—J. Flower with bract.—K. Flower with perianth spread open.—L. Sepal, abaxial view.—M. Petal.—N, O. Trichomes of floral bract apex.

Paepalanthus hippotrichophyllus Herzog, Feddes Repert. Spec. Nov. Regni Veg. 29: 208. 1931. TYPE: Brazil. Amapá: Igarapé Crê-cru of the Rio Oyapock, *Luetzelburg 21408* (holotype, M).

Paepalanthus capillaceus var. *proliferus* Gleason, Bull. Torrey Bot. Club 58: 328. 1931. *Paepalanthus capillaceus* forma *proliferus* (Gleason) Mold., Phytologia 44: 384. 1979. TYPE: Venezuela. Amazonas: Cerro Duida, Central Camp, 4,800 ft., *Tate 552* (holotype, NY).

Paepalanthus capillaceus var. *spiralis* Mold., Mem. New York Bot. Gard. 9: 279. 1957. TYPE: Guyana. Upper Mazaruni River, Karaurieng River, Maipuri Falls, 1,250 m, *Maguire & Fanshawe 32292* (holotype, NY; isotype, M). Note: This taxon, distinguished by its strongly spiral-twisted leaves, is known only from the type locality. Though it may be valid as a variety, it is here regarded conservatively as a synonym.

Plants short-stemmed aquatic perennials, the vegetative portions fully submerged and inflorescences mostly emergent and erect. Main roots abundant, ca. 0.5–1.0 mm diam., much-branched, gray-brown, contorted. Stems up to 7 cm long and 15 mm diam., leafy only near the apex, but the lower portions covered by persistent roots and leaf bases, woolly with brownish hairs. Leaves spirally arranged, pale green to blackish, (2.5–)7–30 cm long, 0.2–0.4 mm wide, the base slightly dilated, ephemerally woolly, coarsely filiform-setaceous, sometimes corkscrew-twisted, the tips acute but usually broken off, glabrous (though often with sand particles and algae adhering in dried material), traversed by a single central vein surrounded by mesophyll (Ruhland, 1903). Inflorescences numerous, synchronous, commonly numbering 10 or more. Peduncle sheaths 3–5 cm long, strongly twisted, glabrous, the apex acuminate, scarious, often lacerate. Peduncles (5.5–)9.0–20.0 cm long, 3-costate or apparently 6-costate by collapse of the centers of the main ribs, glabrous. Capitula 3–5 mm diam., depressed-turbinate to depressed-hemispheric at maturity, sometimes vegetatively proliferating from the center. Involucral bracts in ca. 4 series, both the outer and inner narrowly triangular, subacute to commonly obtuse, erect, the outer ca. 1.1–1.4 mm long, 0.5–0.7 mm wide, the inner 1.9–2.1 mm long, 0.5–0.7 mm wide, about equaling the head; all pale gold-brown to castaneous or nearly black, fleshy or coriaceous-thickened especially toward the base, the margins of at least the inner bracts ± pellucid, shredding with age; glabrous or the inner bracts short-ciliate along distal margins. Floral bracts shorter than or about equaling the flowers, spatulate, obtuse, strongly keeled and somewhat cucullate at apex, cream-colored to pale brown, the apex hirsute abaxially with short subclavate hairs. *Staminate flowers*. Pedicels ca. 0.3–0.5 mm long. Sepals obovate to spatulate, obtuse to rounded, concave, somewhat fleshy, 1.1–1.4 mm long, 0.45–0.6 mm wide, cream-colored to pale gray-brown, ciliate and short-hairy abaxially toward apex. Corolla of 3 separate petals (these separate from earliest visible stage of development), inserted at the base of the androphore (intercalary prolongation of the floral axis above the calyx), or at variable distances above the base, but usually below the insertion of the filaments and pistillodes; the androphore 0.1–0.5 mm long, the petals 1.1–1.5 mm long, 0.4–0.7 mm wide, obtrullate to obovate, rounded toward apex and abruptly apiculate, glabrous. Stamens with filaments 0.7–1.2 mm long, usually inserted at apex of androphore, though occasionally one or more inserted at base, included, the anthers ca. 0.15–0.2 mm long. *Pistillate flowers*. Pedicels 0.2–0.4 mm long. Sepals ovate to elliptic, concave, acute to obtuse, 1.2–1.5 mm long, 0.5–0.8 mm wide, colored as in staminate flowers, short-ciliate from middle to apex and short-hairy abaxially in this region, coriaceous-thickening at maturity, especially at base and sometimes throughout. Petals free, spatulate, usually acute or apiculate, 1.2–1.6 mm long, 0.4–0.6 mm wide, glabrous. Staminodes firm, linear to somewhat broad and nearly scalelike, 0.2–0.6(–1.4) mm long. Ovary with a few scattered hairs at base, 0.4–0.7 mm long, the style 0.1–0.4 mm long, the appendages 0.4–0.5 mm long, the stalk thick, the papillose portion orange-brown, darker than the stalk, the style branches diverging at the same level as the appendages, 0.7–0.9 mm long, bifid half to nearly all their length. Floral trichomes clavate and thick-walled with dense granular thickening of the internal wall.

Phenology. Collected in flower year-round.

Habitat and distribution. Adhering to rocks of streambeds in rapidly flowing water, 100–1,600 m. Venezuela. Amazonas: Cerros Duida and Marahuaca south to Neblina; Bolívar: Gran Sabana. Guyana: Upper Mazaruni River and Kaieteur Plateau. Brazil. Amazonas: Serra Aracá; Amapá: Rio Oyapock (Oiapoque).

Additional specimens examined. VENEZUELA. AMAZONAS: Cerro Duida, *Fariñas et al. 420* (NY), *Maguire & Maguire 29153* (MO, NY), *Maguire et al. 29611* (NY); *Tillett et al. 751-82* (NY); Cerro Marahuaca, *Steyermark & Holst 130470* (MO); Cerro Aracamuni, *Liesner & Carnevali 22308* (MO), *Wurdack & Adderley 43602* (NY); base of Cerro Neblina, *Davidse & Miller 27038* (MO), *Gentry & Stein 46937* (MO), *Liesner 15737* (MO); *Liesner 16653* (MO). BOLÍVAR: Canaima, *Schnee 1745* (MO); Río Yuné, ESE of Churitepui, *Huber 9764* (MO); headwaters of Río Venamo,

NW of Cerro Venamo, *Steyermark & Nilsson 16* (NY); Salto El Danto, *Knapp & Mallet 6711* (MO, NY), *Holst et al. 2117* (MO); Salto el Torón, *Thomas 2529* (NY); W of Sororopán-tepui, *Steyermark 60208* (F); Kavanayén, *Kral 70411* (MO), *Moore et al. 9836* (NY); upper Río Aponguao, NW of Parupá, *Kral 72046* (MO); Río Aponguao, *Trujillo 11599* (NY); 10 km SW of Karaurín-tepui, *Liesner 23486* (MO); Río Kamá, *Steyermark & Liesner 127619* (MO); Rio Cauí, *Luteyn et al. 6323* (F, MO); Salto Yuruani, *Kral 70570* (MO), *Kral 72131* (MO). GUYANA. Upper Mazaruni, Utschi River, *Tillett & Tillett 45793* (MO); Upper Mazaruni, Kamarang River, Mt. Aymatoi, *Maas et al. 5731* (MO); Kaieteur Plateau, *Maguire & Fanshawe 23243* (MO). BRAZIL. AMAZONAS: Serra Aracá, *Prance et al. 29150* (MO).

Rondonanthus capillaceus is distinguished from all other species of the genus by its aquatic habit and filiform-setaceous leaves exceeding the peduncles. Its flowers differ from those of other species in several respects. The perianths lack black pigmentation and are short-hairy at the apex rather than long-ciliate. The granular ornamentation of the trichome internal wall is also exceptional and similar to that found in *Paepalanthus*. In the staminate flowers, an androphore is present, and the petals are usually free from the earliest stages of development.

It is here placed in *Rondonanthus* because of similarities in root and peduncle sheath morphology and involucral bract shape, and because of the presence of long linear staminodes in most material. (These are small and scalelike in a few populations.) The bifid stigmas in combination with long hairs at the base of the ovary also suggest *Rondonanthus*.

This species has the largest distribution of any in the genus, with a disjunct population in Amapá, Brazil. These plants, described by Herzog (1931) as *Paepalanthus hippotrichophyllus*, are mistakenly reported to have tubular corollas in the staminate flowers.

Rondonanthus capillaceus is highly convergent with *Leiothrix fluitans* (C. Martius) Ruhl. of Minas Gerais, Brazil, another submerged aquatic of rapidly flowing water. The species have similar vegetative morphology and both have free petals in both pistillate and staminate flowers, suggesting that this floral modification may be somehow at least incidentally correlated with adaptation as an aquatic. They are distinguished primarily by the structure of the gynoecium and by the presence or absence of staminodes.

Rondonanthus caulescens (Mold.) Hensold & Giulietti, comb. et stat. nov. *Paepalanthus jauensis* var. *caulescens* Mold., Phytologia 44: 215. 1979. TYPE: Venezuela. Bolívar: Cumbre de Aprada-tepui, 2,460–2,500 m, 25 Feb. 1978, *Steyermark et al. 115893* (holotype, LL; isotypes, F, MO).

Plants short-stemmed, cespitose perennials. Main roots ca. 0.5 mm diam., sparingly branched, pale orange-brown. Stems 4–6 cm long at flowering, ca. 2–3 mm diam., leafy to the base, woolly with cream-colored hairs. Leaves spirally arranged, 3–4 cm long, 0.6–1.0 mm wide; the bases somewhat dilated, broadest below, scarious, densely woolly; the blades linear, sharply acute, rigid, glabrous, 3–5-veined, the veins of equal size. Inflorescences single per age class, the old ones often persistent on stem. Peduncle sheaths 4–5 cm long, twisted, glabrous, the apex sharply acute to acuminate, green, often lacerate with age. Peduncles 15–35 cm long, 3-costate, pubescent with retrorse malpighian hairs especially toward apex, and long filamentous hairs fringing the base of the capitulum. Capitula 7.5–10 mm diam., turbinate to hemispheric at maturity. Involucral bracts in 3 series, the outer narrowly triangular, acute, spreading, ca. 2.3–2.7 mm long, 0.5–0.8 mm wide at base, the inner bracts elliptic to oblanceolate, acuminate, erect, ca. 4.5 mm long, 1.3–1.4 mm wide, equaling the head or surpassing it slightly (up to 0.5 mm); the outer bracts gold-brown, often with some irregular blackish streaks, the inner mostly black with a paler tip and distal midvein; the outer and inner bracts ciliate to the base and also hirsute abaxially, the inner tufted at the apex. Floral bracts slightly exceeding the flowers, linear-oblanceolate, acuminate, creamy hyaline and flecked with black distally, tufted abaxially at apex. *Staminate flowers*. Pedicels 1.3–1.5 mm long. Sepals obovate-elliptic, acuminate, ca. 2.2–3.0 mm long, 0.8–1.0 mm wide, hyaline with black flecks, sometimes appearing gray except for pale base and apex, the apex tufted abaxially with divergent-ascending trichomes. Corolla connate into a 3-lobed tube, the androphore lacking, the tube ca. 2.3–2.8 mm long, the lobes triangular-obtuse, the upper margin ciliate, involute, and retracting the stamens after anthesis. Stamens with filaments adnate to corolla at base, included; anthers ca. 0.35 mm long. *Pistillate flowers*. Pedicels ca. 0.8 mm long. Sepals ovate-elliptic, concave, acuminate, 2.8–3.2 mm long, ca. 0.8–1.1 mm wide, cream-colored or slightly grayish, pubescent as in the staminate flowers, not observed in mature condition. Petals connate in distal half, the segments oblong, triangular-obtuse at apex, ca. 2.5–3.0 mm long, 0.5 mm wide, ciliate at upper margin and also pilose abaxially in submarginal bands. Staminodes linear, 0.6–0.9 mm long. Ovary ringed by hairs at base, 0.5

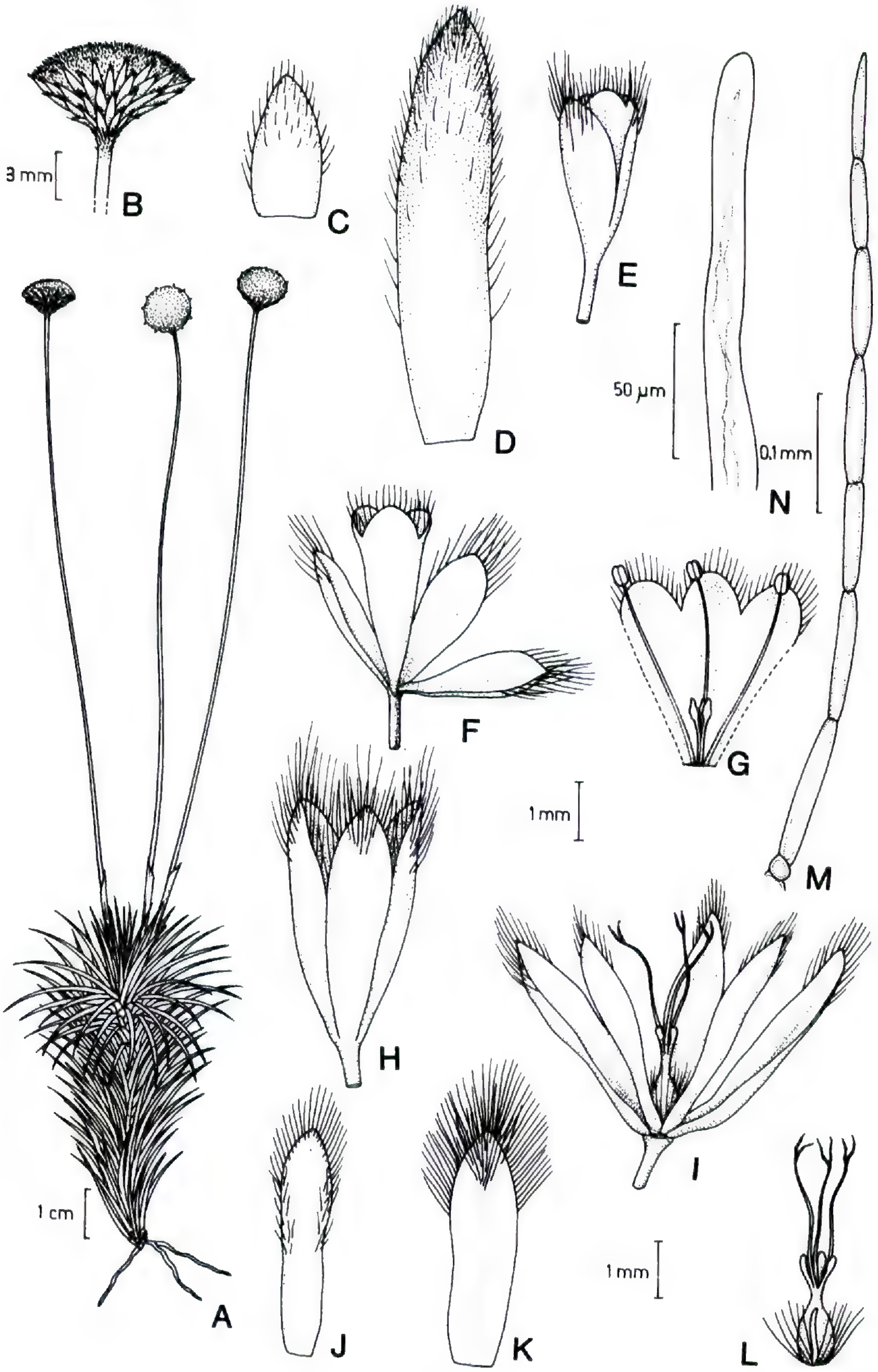


FIGURE 3. *Rondonanthus duidae* (Gleason) Hensold & Giulietti (*Steyermark 58319* MO).—A. Habit.—B. Inflorescence.—C, D. Involucral bracts, lower and upper. E–G. Staminate flower.—E. Flower.—F. Flower with sepals spread apart.—G. Corolla, opened to show stamens and pistillodes. H–L. Pistillate flower.—H. Flower.—I. Flower with perianth spread apart.—J. Petal, adaxial view.—K. Sepal, abaxial view.—L. Gynoecium, shown with subtending hairs and a staminode.—M, N. Trichomes of floral bract apex.

mm long, the style 0.3 mm long, the appendages ca. 0.4 mm long, the stalk rather thick, the papillose portion pale orange, the style branches diverging slightly above the appendages, 2.5 mm long, bifid. Floral trichomes subacute, lacking granular thickening of the internal wall.

Phenology. Collected in flower in February.

Habitat and distribution. Known only from the type; no habitat information given.

This species appears more similar to *R. acopanensis* of the Chimantá Massif than to "*P. jauensis*" (here included in *R. duidae*), with which it occurs sympatrically at Aprada-tepui, and of which it was originally described as a variety. It is allied with *R. acopanensis* by the acuminate, colorless apices of the involucral bracts and perianth, and by the more densely woolly leaf bases which are broadest at the base.

Rondonanthus duidae (Gleason) Hensold & Giulietti, comb. nov. *Paepalanthus duidae* Gleason, Bull. Torrey Bot. Club 58: 329. 1931. TYPE: Venezuela. Amazonas: summit of Mount Duida, 5,500–6,000 ft., *Tate 456* (holotype, NY). Figure 3.

Syngonanthus phelpsae var. *pilosus* Mold., Mem. New York Bot. Gard. 9: 282. 1957. TYPE: Venezuela. Amazonas: Cerro de la Neblina, W escarpment, 1,850–1,900 m, *Maguire et al. 37308* (holotype, NY; isotype, F). Syn. nov.

Syngonanthus phelpsae var. *viridis* Mold., Phytologia 22: 126. 1971. TYPE: Venezuela. Amazonas: Cerro de la Neblina, Planicie de Zuloaga, 2,300 m, *Steyermark 103840* (holotype, NY; isotype, LL). Syn. nov.

Paepalanthus jauensis Mold., Mem. New York Bot. Gard. 23: 850, fig. 5. 1972. TYPE: Venezuela. Bolívar: Cerro Jaua, cumbre de la porción centro-oeste, 1,900–2,100 m, *Steyermark 97906* (holotype, LL). Syn. nov.

Paepalanthus duidae var. *parvifolius* Mold., Phytologia 54: 121. 1983. TYPE: Venezuela. Amazonas: Cerro Marahuaca, 2,750 m, *Tillett et al. 752-349* (holotype, NY). Syn. nov.

Plants rosulate or short-stemmed cespitose perennials, rarely branching above the base. Main roots 0.5–1.0 mm diam., sparingly branched, cream to pale orange. Stems up to 10 cm long, occasionally up to 40 cm long but then sterile, ca. 2–5 mm diam., densely leafy to the base, woolly with light brown hairs. Leaves spirally arranged, 1.5–15 cm long, 0.3–1.5 mm wide; the base slightly dilated just below the blade and then usually constricted proximally, pubescent with long matted feltlike hairs as on the stem; the blades linear to acicular, usually sharp-cuspidate, subterete and rigid to flat and chartaceous, glabrous to densely pubescent with retrorse malpighian hairs, usually with the midvein on the lower surface prominently thickened in contrast to the two narrow lateral veins (occasionally leaves merely acute and midvein similar in thickness to laterals). Inflorescences about 1–4 per age class, the old ones often persistent on stem. Peduncle sheaths 2–6.5 cm long, twisted, pubescent like the leaves, the apex acuminate, scarious. Peduncles (6–)11–39 cm long, 6-costate, pubescent with retrorse malpighian hairs to nearly glabrous, usually with long filamentous hairs fringing the base of the capitulum. Capitula 6–14 mm diam., hemispheric at maturity. Involucral bracts in 4–6 series, the outer ovate to narrowly triangular or lanceolate, subacute, often recurved, 0.5–4.0 mm long, 0.4–1.2 mm wide at base, the inner bracts truly oblanceolate though appearing lance-linear to lanceolate in their exposed portions, tapered to an acute or narrowly rounded apex, erect or somewhat spreading, 2.5–8.5 mm long, 0.6–1.5 mm wide, often surpassing the head, sometimes by as much as 3–4 mm; variable in color, ranging from uniform deep brown with a dark reddish midvein to blackened only along the distal margins of the inner bracts with the outer bracts and medial areas of the inner bracts a strongly contrasting pale gold; glabrous or often ciliate, and then often hirsute abaxially (rarely also adaxially) at apex. Floral bracts commonly equaling or slightly surpassed by the flowers, linear to linear-oblanceolate, acute to subacute, blackened distally, bearded with long hairs abaxially at apex. *Staminate flowers.* Pedicels 0.5–1.5 mm long. Sepals broadly spatulate, rounded to acute, and sometimes the upper margin lacerate, 1.5–2.7 mm long, 0.6–1.2 mm wide, uniformly blackened distally, white below, rarely dark brown distally, grading into a lighter brown (Cerro Jaua and Sarisariñama), bearded abaxially with long erect trichomes. Corolla connate into a 3-lobed tube, or the petals very rarely free from each other, the androphore lacking, the tube 2.0–3.0 mm long, the lobes rounded and sometimes (Aprada-tepui) the sinuses rather deep, almost equaling the tube in length, the upper margin and abaxial lobe apices densely pilose, involute after anthesis. Stamens with filaments adnate to corolla at base, usually exsert; anthers ca. 0.2–0.3 mm long. *Pistillate flowers.* Pedicels 0.4–1.5 mm long. Sepals broadly elliptic to ovate-elliptic, concave, acute, 2.0–4.2 mm long, 1.0–1.5 mm wide, cream-colored or sometimes pigmented as in staminate flowers toward the apex though usually much less so, ciliate for most of their length and bearded at the apex as in the staminate flowers, thickening at base at maturity. Petals mostly free, rarely briefly connate distally, oblong to subspatulate, obtuse to acute, 2.0–3.5 mm long, 0.5–1.5 mm wide, densely ciliate at upper margin and frequently also pilose abaxially at apex or in submarginal bands. Staminodes linear, 0.2–2.0 mm long. Ovary ringed by hairs at base, 0.5–0.8 mm long, the style 0.2–0.6 mm long, the appendages ca. 0.6–1.0 mm long, the stalk usually

long and narrow, up to ⅔ the total length, the papillose portion white, sometimes collapsing after anthesis and appearing nearly filiform, the style branches diverging slightly above the appendages, 1.5–2.5 mm long, bifid, though in many cases the two segments cohering. Floral trichomes subacute to rounded, lacking granular thickenings of the internal wall.

Phenology. Collected in flower mostly from September to February, rarely in March and June.

Habitat and distribution. Locally abundant on open plateaus with shallow, rocky, wet soils, at 1,600–2,800 m. Venezuela. Amazonas: summits of Cerros Marahuaca, Duida, and Neblina; Bolívar: summits of Cerros Jaua, Sarisariñama, and Aprada-tepui.

Additional specimens examined. VENEZUELA. AMAZONAS: summit of Cerro Duida, *Steyermark 58319* (F, MO, NY, VEN), *Steyermark 58361* (F, NY); Cerro Duida, summit of Peak 7, *Tate 625* (NY); Cerro Duida, Caño Sapo, *Tate 691* (NY); Cerro Marahuaca, SE section, *Maguire et al. 65637* (MO, NY), *Maguire et al. 65638* (MO, NY, VEN), *Maguire et al. 65639* (MO, NY); Cerro Marahuaca, NW section, *Steyermark et al. 124366* (MO, NY), *Steyermark et al. 124469* (NY); Cerro Marahuaca, extreme SE section, *Steyermark 129109* (LL, MO); Cerro Marahuaca, extreme NE section, *Steyermark 129191* (MO, VEN), *Steyermark & Delascio 129247* (LL); Cerro Marahuaca, central part of the SE Meseta, *Steyermark 129475* (LL, MO); Cerro Marahuaca-huha, *Steyermark 125932* (LL, VEN); Cerro Marahuaca–Fhuif, *Steyermark et al. 126099* (LL); Cerro Marahuaca–Atuhua–Shiho (SW of Cerro Marahuaca), *Steyermark 126295* (LL, VEN); Cerro de la Neblina, Rio Yatua, *Maguire et al. 36930* (NY), *Maguire 37123* (NY, VEN), *Maguire et al. 42261* (F, NY, VEN), *Maguire et al. 42279* (F, NY, VEN); NW plateau, *Liesner 16028* (MO), *Liesner 16046* (MO); Planicie de Zuloaga, Río Titirico, *Steyermark 103878* (NY), *Steyermark 103920* (NY). BOLÍVAR: Macizo de Sarisariñama, *Fernandez 4753* (MO, PORT); Aprada-tepui, *Steyermark 115885* (F, MO, VEN); S section, 30 km E of Urimán, *Huber 9539* (MO).

The amount of variation in *Rondonanthus duidae* is very high, with some of the variation geographically distributed, and some probably environmental, such as leaf length and width, which can vary considerably within a single population. Involucral bract color varies geographically. The plants of Cerro Marahuaca, Aprada-tepui, and some of Cerro de la Neblina have uniformly black involucres, while plants of Duida and some of Neblina have highly contrasting gold and black or almost entirely gold bracts. Plants of Jaua and Sarisariñama have more rounded bract apices, and lack characteristic black color to bracts and perianth, having a dull brown color instead. Plants of Aprada-tepui are distinguished by very long black involucral bracts and by *Syngonanthus*-like fusion of the petals of the pistillate flower corolla.

This species is closely related to *Rondonanthus roraimae*, from which it can only be satisfactorily distinguished by reference to flower morphology. In general, the leaves of *R. duidae* also differ from those of *R. roraimae* by the prominent midvein and aristate tip, but this character is lacking in some collections (Aprada-tepui and some of Neblina).

Rondonanthus duidae is also habitally similar to *S. duidae* Mold., with which it is sympatric. These species are so similar in general aspect that two collections of *R. duidae* have been described as new varieties of *S. phelpsae* (now placed in *S. duidae*). At Neblina some plants look intermediate with *S. duidae*, with rather short, unevenly blackened involucral bracts, with the sepal apices sharply acute-lacerate and bearded below the apex, but not at the apex (as in *S. duidae*), the corolla of the staminate flower developing rather irregularly, and the gynoecium intermediate with a rather long common style and style branches apparently fine and simple, not bifid. This is particularly true of the type of *S. phelpsae* var. *pilosus* Mold. It is possible that hybridization is occurring at Neblina, although *S. duidae* has never been collected south of Cerro Aracamuni.

Another possible hybrid requiring more study is the type of *Paepalanthus fraternus* var. *radiatus* Mold. (Phytologia 49: 383–386. 1981) from Cerro Marahuaca. The leaves of this plant are dull green and rounded at the apex rather like the sympatric species *Paepalanthus parvicephalus* (Mold.) Hensold, but have a cartilaginous texture, and are rosulate. The peduncles are of variable lengths, and the lanceolate radiating involucral bracts and soft heads which flatten upon pressing suggest *R. duidae*. The flowers are intermediate between the two taxa, with some developmental irregularities, particularly in the gynoecium.

Rondonanthus flabelliformis (Mold.) Hensold & Giulietti, comb. nov. *Wurdackia flabelliformis* Mold., Mem. New York Bot. Gard. 9: 413. 1957. TYPE: Venezuela. Bolívar, Chimantá Massif, Torono-tepui, 2,165–2,180 m, *Steyermark & Wurdack 671* (holotype, NY; isotypes, F, K). Figure 4.

Plants caulescent perennials. Main roots ca. 1–1.5 mm diam., sparingly branched, pale orange-brown. Stems up to 16 cm long, densely leafy to the base, woolly with grayish hairs. Leaves distichous, 9–10 cm long, 5–8 mm wide; the bases

slightly dilated linear or broader below, densely woolly with matted whitish hairs; the blades ligulate-falcate, obtuse to rounded, rigid, shiny, glabrous, ca. 30-veined, the veins of equal size, the margins pale and slightly revolute. Inflorescences up to 4 per age class. Peduncle sheaths ca. 6 cm long, not twisted, glabrous, the apex acute, green or somewhat scarious. Peduncles 13–16 cm long, 7–8-costate, pubescent with retrorse malpighian hairs between costae, and long filamentous hairs fringing the base of the capitulum. Capitula 15–19 mm diam., hemispheric to subglobose at maturity. Involucral bracts in 5 series, the outer triangular, acute, ca. 4 mm long, ca. 1.0 mm wide at base, the inner bracts spatulate, rounded and minutely apiculate, ca. 6 mm long, 1.5 mm wide, about equaling the head; the outer bracts gold-brown, coriaceous, the inner black, chartaceous, except for the gold-brown midvein; the outer bracts glabrous, the inner bearded abaxially at the apex, glabrate with age. Floral bracts about equaling the flowers, spatulate, obtuse, the distal half blackened, bearded abaxially at apex. *Staminate flowers.* Pedicels not measured. Sepals oblong-obovate, rounded and apiculate, ca. 2.7–2.9 mm long, ca. 0.7–0.8 mm wide, blackened distally, bearded abaxially with long, erect trichomes. Corolla connate into a 3-lobed tube at first, the segments later separating at least at the base, the androphore lacking; the tube 3.3 mm long, the lobes rounded, the upper margin and abaxial lobe apices ciliate-pilose, involute after anthesis. Stamens with filaments adnate to corolla, included; anthers ca. 0.3–0.35 mm long. *Bisexual flowers.* Pedicels ca. 2 mm long. Sepals ovate, concave, obtuse, ca. 4 mm long, 1.3 mm wide, cream-colored, bearded as in the staminate flowers, thickening at base at maturity. Petals connate into a tube except at base, the segments spatulate, ± rounded at apex, ca. 3.5 mm long, 1.0–1.2 mm wide, densely long-ciliate at upper margin. Stamens present, opposite the petals, similar to those of the staminate flowers, but with the filaments slightly shorter. Ovary with no hairs at the base, ca. 0.5 mm long, the style 0–0.3 mm long, the appendages ca. 0.5 mm long, the stalk thick, the papillose portion brownish, the style branches diverging slightly above the appendages, ca. 2 mm long, conspicuously bifid. Floral trichomes subacute to rounded, lacking granular thickenings of the internal wall.

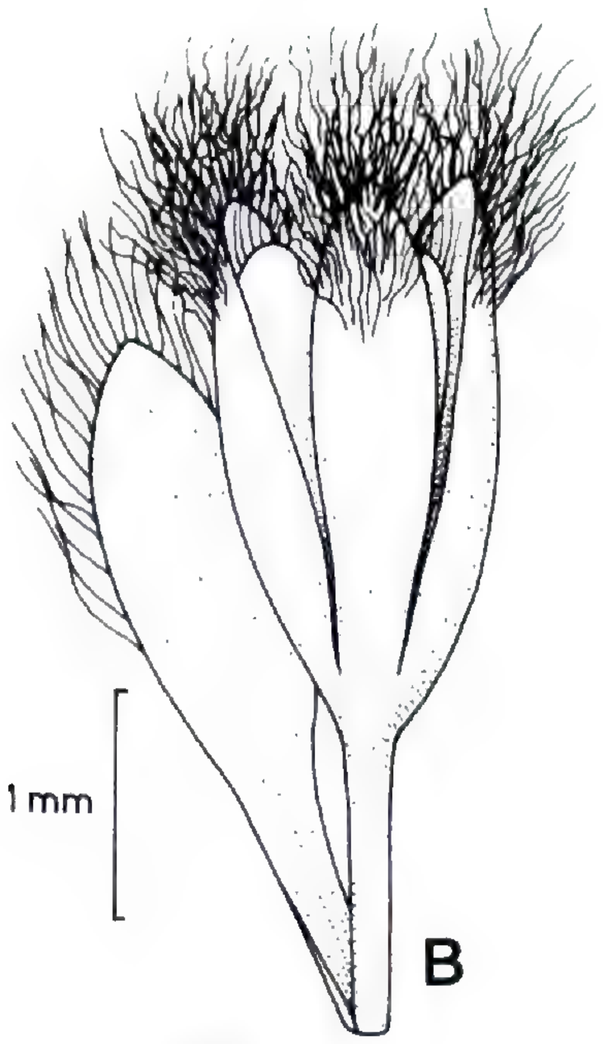
Phenology. Collected in flower in February.

Habitat and distribution. Known only from the type, reported as locally frequent in a *zanjon* (large crevice), in moist places among rocks.

Rondonanthus flabelliformis is clearly closely related to *R. acopanensis*, differing in the persistence of the leaves along the stem, in the very large size of the leaves and capitula, and in the occurrence of stamens in the morphologically pistillate flowers. It would be of great interest to determine the relationship between these two species. It is possible that *R. flabelliformis* has been derived from *R. acopanensis* by macromutation, a suspicion supported by the occurrence in the latter species of discontinuous size classes. Alternatively, it may be postulated as a primitive relict, with the persistent leaves and bisexual flowers representing an ancestral condition.

Rondonanthus roraimae (Oliver) Herzog, Feddes Repert. Spec. Nov. Regni Veg. 29: 210. 1931. *Paepalanthus roraimae* Oliver, Trans. Linn. Soc. London, Bot. 2: 286. 1887. TYPE: Guyana. Mount Roraima, 15 Dec. 1884, *Thurn 294* (holotype, K). Figure 5.

Plants rosulate or caulescent cespitose perennials. Main roots ca. 0.3–0.7 mm diam., sparingly branched, cream to pale orange. Stems up to 10 cm long, 2–3 mm diam., leafy to the base, woolly with light brown hairs. Leaves spirally arranged, 1.5–4 cm long, 0.5–1.3 mm wide; the base slightly dilated just below the blade and then usually constricted below, pubescent with long matted feltlike hairs as on the stem; the blades linear to acicular, the apex rounded or bluntly cuspidate, subterete and rigid to flat and chartaceous, glabrous or sparingly pubescent with retrorse malpighian hairs, especially abaxially, and then usually glabrate, 3-veined, the veins of equal size. Inflorescences 1(–5) per age class. Peduncle sheaths 3–4(–6) cm long, twisted, pubescent like leaves, the apex usually erose-toothed, scarious, eventually lacerate. Peduncles 5–28 cm long, 6–10-costate, pubescent with retrorse malpighian hairs to nearly glabrate, usually with long filamentous hairs fringing the base of the capitulum. Capitula 8–13 mm diam., hemispheric at maturity. Involucral bracts in 4–5 series, the outer ovate-triangular to lanceolate, subacute, often recurved, 2.3–3.7 mm long, 0.8–1.2 mm wide at base, the inner bracts lanceolate to oblanceolate and then appearing lance-linear to lanceolate in their exposed portions, tapered to an acute or subacute apex, erect or somewhat spreading, 4.5–7.0 mm long, 1.0–1.5 mm wide, surpassing the head by 1–2.5 mm; the outer bracts mostly castaneous, or sometimes fuscous along the margins, progressively darker above, the innermost bracts commonly deep fuscous with only the mid-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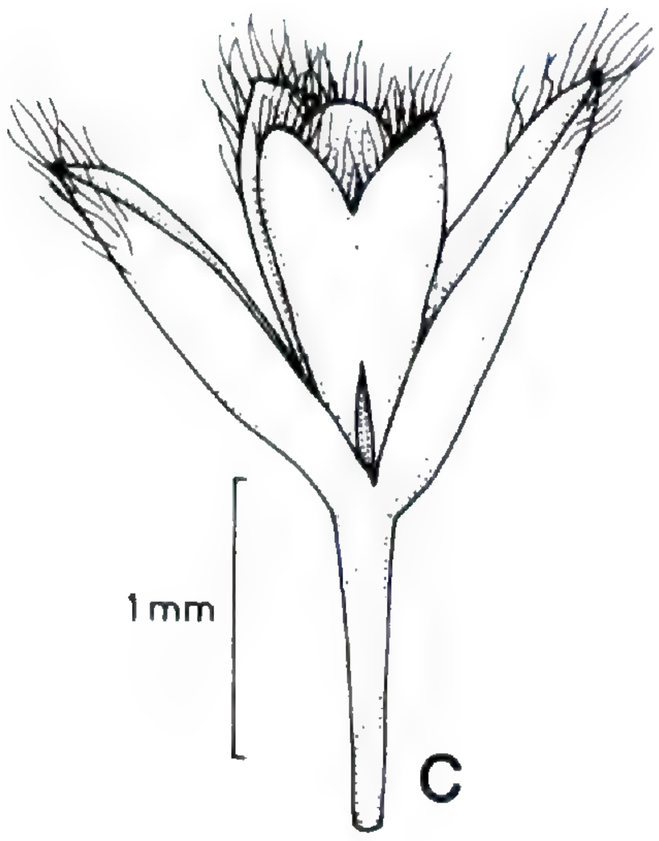
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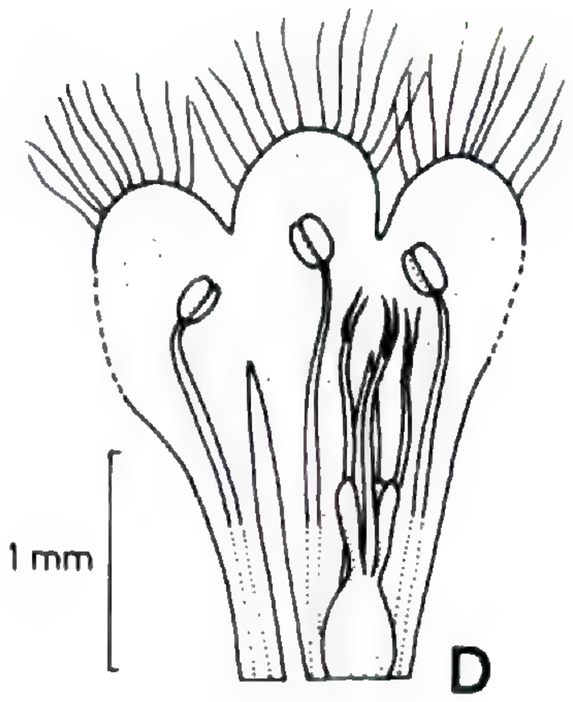
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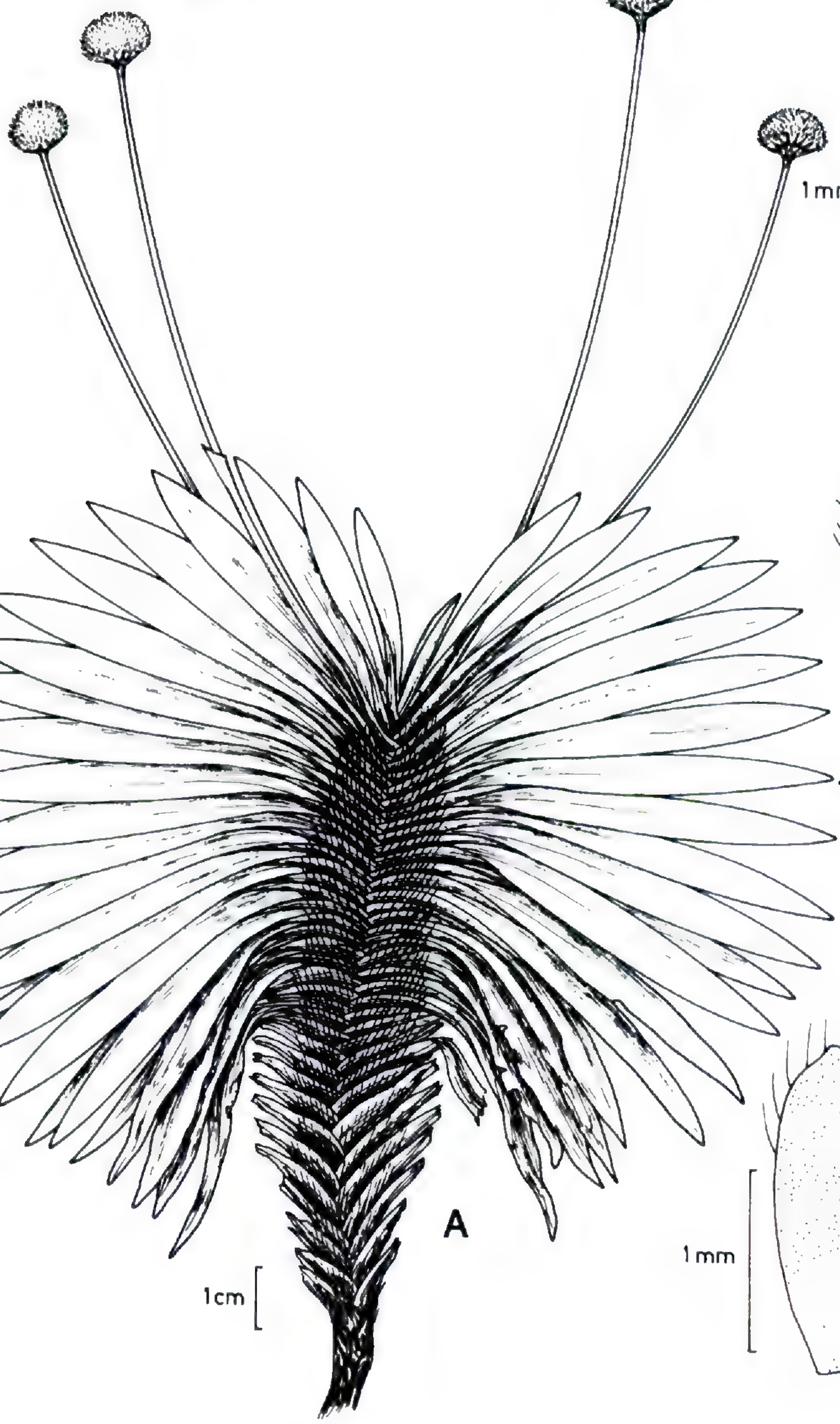
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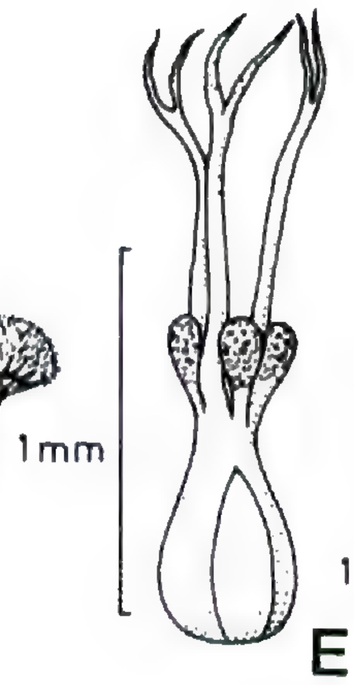
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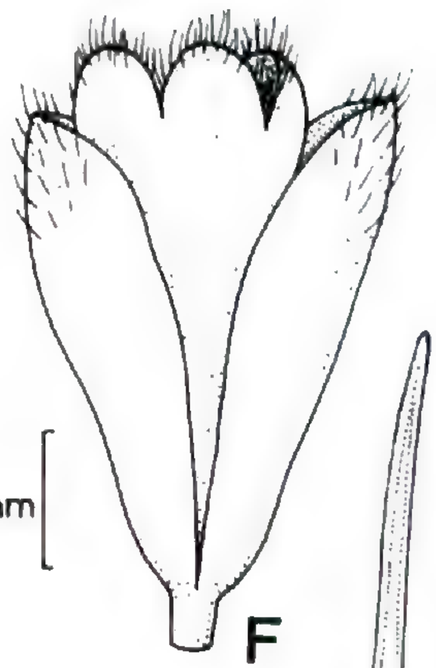
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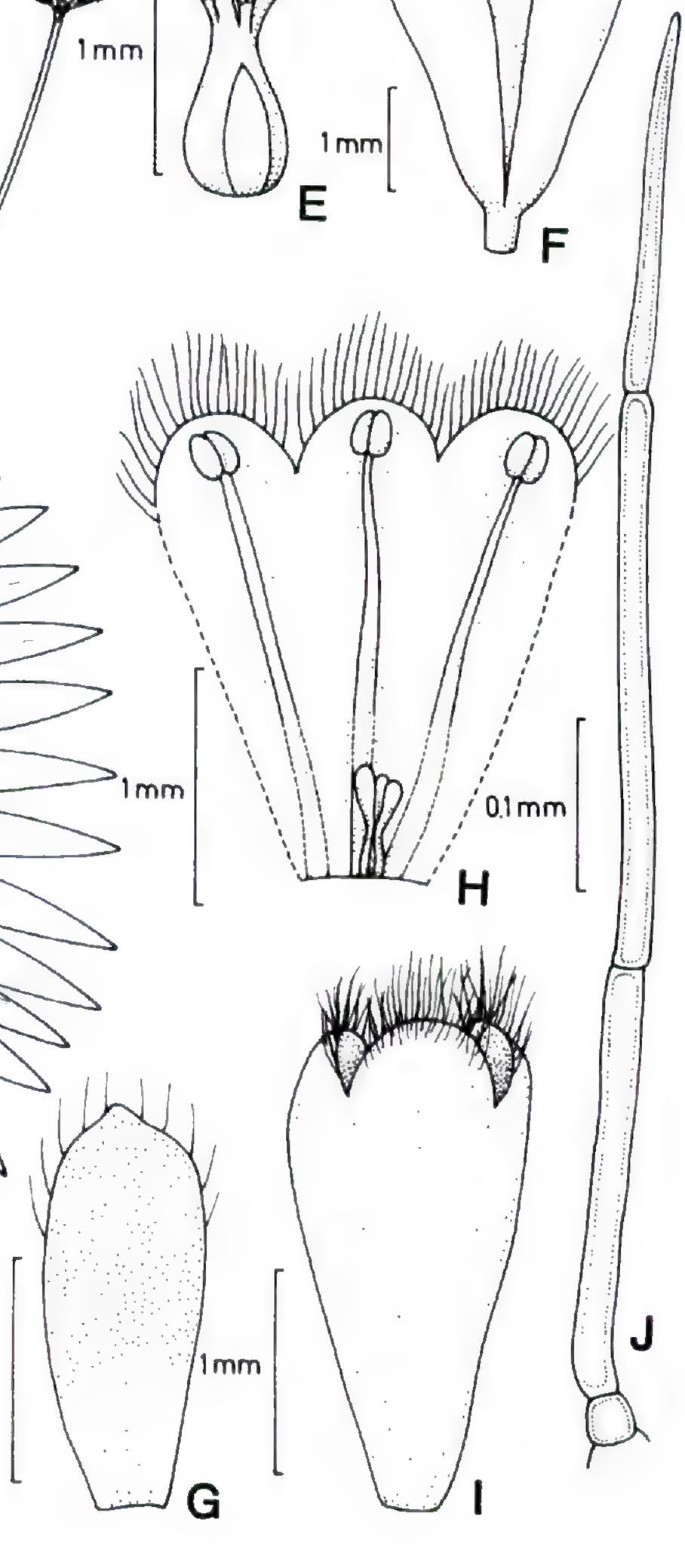
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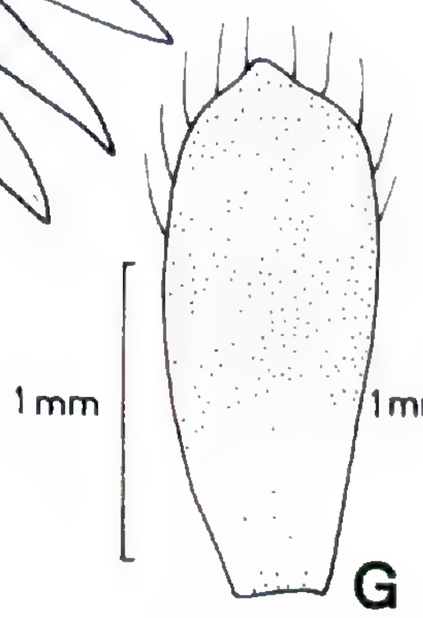
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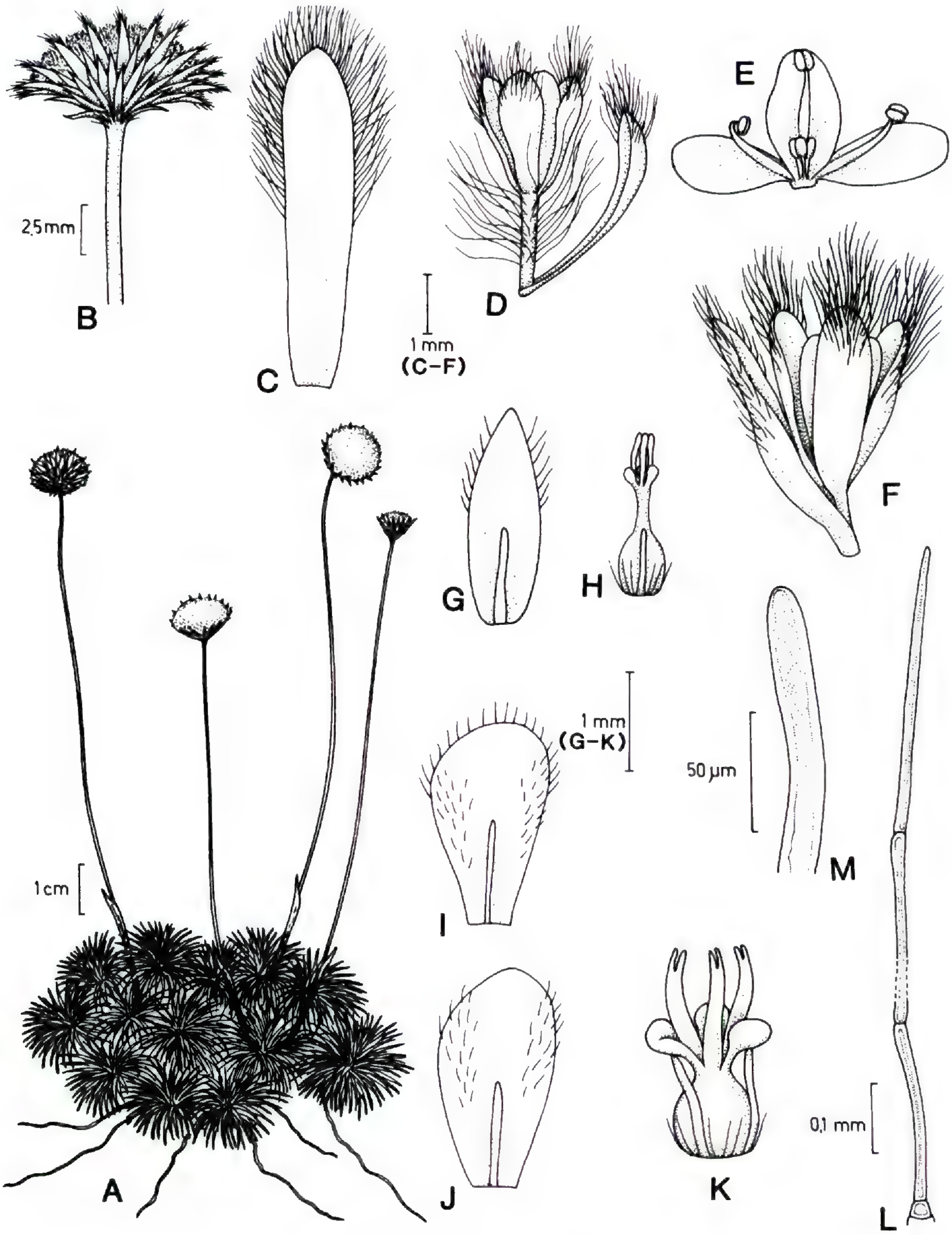

FIGURE 5. *Rondonanthus roraimae* (Oliver) Herzog (*Liesner 23239* MO, unless stated otherwise).—A. Habit.—B. Inflorescence.—C. Involucral bract, adaxial view. D, E. Staminate flower.—D. Flower with bract.—E. Corolla, opened, with stamens and pistillodes. F–K. Pistillate flower.—F. Flower with bract.—G. Petal, adaxial, with staminodes.—H. Gynoecium, with staminodes and subtending hairs. I–K. Large-flowered morph (*Aymard 2480* PORT).—I, J. Petals with staminodes.—K. Gynoecium, with staminodes and hairs.—L, M. Trichomes of floral bract apex.

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FIGURE 4. *Rondonanthus flabelliformis* (Mold.) Hensold & Giulietti (*Steyermark & Wurdack 671* NY).—A. Habit. B–E. Bisexual flower.—B. Flower.—C. Flower with sepals spread apart.—D. Corolla opened to show functional stamens and gynoecium.—E. Gynoecium. F–I. Staminate flower.—F. Flower (pedicel broken).—G. Sepal, adaxial view.—H. Corolla, opened to show stamens and pistillodes.—I. Corolla, entire.—J. Trichome of floral bract apex.

vein castaneous; usually densely and persistently ciliate, the inner also commonly hirsute abaxially along the margins, rarely tufted at apex, occasionally glabrate. Floral bracts commonly equaling the flowers, linear, acute to subacute, blackened distally, bearded abaxially with long hairs. *Staminate flowers.* Pedicels 1.0–2.5 mm long. Sepals broadly oblanceolate to obovate, rounded to acute, 1.5–2.5 mm long, 0.5–1.3 mm wide, uniformly blackened distally, white below, bearded abaxially with long erect trichomes. Corolla connate at first into a 3-lobed tube, but the segments separating before anthesis, the androphore lacking; the petal segments 1.9–2.5 mm long, 0.9–1.5 mm wide, obovate, rounded to subacute, glabrous. Stamens with filaments adnate to corolla at base, included; anthers ca. 0.3–0.4 mm long. *Pistillate flowers.* Pedicels 0.9–1.3 mm long. Sepals obovate to spatulate, concave, acute to obtuse, 1.5–2.1 mm long, 0.6–1.8 mm wide, of the same color and pubescence as in the staminate flowers, thickening at base at maturity. Petals free, ± obovate, rounded to apiculate, 1.5–2.1 mm long, 0.6–1.2 mm wide, sparingly ciliate along lateral margins below apex, and frequently also pilose abaxially in submarginal bands. Staminodes linear, 0.5–1.2 mm long. Ovary ringed by hairs at base, 0.5–0.7 mm long, the style ca. 0.3 mm long, the appendages ca. 0.4–0.5 mm long, the stalk narrow, the papillose portion white, the style branches diverging slightly above the appendages, ca. 1.0–1.2 mm long, bifid though the two segments often failing to separate. Floral trichomes rounded to clavate, lacking granular thickenings of the internal wall, though sometimes lightly flecked.

Phenology. Collected in flower mostly June to September, occasionally April and March.

Habitat and distribution. In open rocky or boggy, often partially inundated areas over thin soils or rock, 2,300–2,800 m. Venezuela. Bolívar: summits of Mount Roraima, Kukenán-tepui, Yuruani-tepui, and Ilú-tepui. Guyana: summit of Mount Roraima.

Additional specimens examined. VENEZUELA. BOLÍVAR: Ilú-tepui, NW sector (Tramén-tepui), *Huber 10065* (NY); Yuruani-tepui, *Huber 11813* (MO); Kukenán-tepui, *Huber & Alarcon 10526* (MO), *Liesner 23069* (MO); summit of Mount Roraima, *Aymard & Luteyn 2480* (NY, PORT), *Bechine 92* (MY), *Hernandez 1* (MY), *Steyermark 58799* (F, NY, VEN), *Steyermark 112438* (F, NY), *Steyermark 112608* (VEN). GUYANA. MAZARUNI-POTARO: summit of Mount Roraima, *Abbensetto 8* (K), *Connell & Quelch 660* (K, NY), *Liesner 23239* (MO), *Liesner 23316* (MO), *Luetzelburg 21605* (NY), *Quelch & Connell 102* (K, NY), *Quelch & Connell 315* (K), *Tate 372* (NY).

Rondonanthus roraimae, as the type of the genus, was originally described as dioecious and having free petals in both pistillate and staminate flowers. Though the trend to dioecy is pronounced, monoecious plants are occasionally found. In addition, petal fusion in staminate flowers is found to occur early in development, although in older, postanthesis flowers, which are easier to dissect and interpret, the petals are invariably free.

The species, endemic to the Roraima formation of eastern Venezuela, is very similar to *R. duidae,* found to the west. *Rondonanthus roraimae* can be distinguished by the glabrous, ephemerally fused corolla segments of the staminate flowers, and also usually by leaf characters (see *R. duidae*). Other characters distinguishing *R. roraimae* are the included stamens with fleshy filaments and larger anthers, as well as the much shorter (but not narrower) petals, style branches, and appendages in the pistillate flowers. These characters, together with the more swollen floral trichome apices, all suggest polyploidy. (A similar suite of characters distinguishes the tetraploid *P. mollis* var. *itambeensis* Hensold from *P. mollis* Kunth var. *mollis*; Hensold, 1988). In addition, *R. roraimae* blooms earlier in the year than *R. duidae.*

Excluded Species

Rondonanthus micropetalus Mold., Fieldiana, Bot. 28: 126. 1951. TYPE: Venezuela. Bolívar: Mount Roraima, SW-facing side, *Steyermark 58777* (holotype, NY; isotype, F).

This species is an abnormal form of *Paepalanthus roraimensis,* with dwarf peduncles and abnormal floral development. In the material observed, the staminate corollas were abortive and underdeveloped, represented only by small lobes of tissue on the floral axis, which were apparently interpreted as free petals.

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SYNONYMIZATION OF THE GENERA *COMANTHERA* AND *CARPTOTEPALA* WITH *SYNGONANTHUS* (ERIOCAULACEAE)[1]

Ana Maria Giulietti[2] *and*
Nancy Hensold[3]

ABSTRACT

The systematic positions of the monotypic Guayanan genera *Carptotepala* Mold. and *Comanthera* Lyman B. Smith are reevaluated. *Carptotepala jenmanii* (Gleason) Mold. is here placed in *Syngonanthus* sect. *Thysanocephalus* near *S. xeranthemoides*, under the name *S. jenmanii* (Gleason) Giulietti & Hensold. *Comanthera kegeliana* (Koern.) Mold. is here returned to *Syngonanthus* sect. *Eulepis*, as *S. kegelianus* (Koern.) Ruhl. Synonymies are given for each species.

The Eriocaulaceae, as currently treated, comprise 13 genera and about 1,200 species (Kral, 1989). The family has a pantropical distribution but is much more diverse and species-rich in South America, where two disjunct centers of diversity occur. These are the Cadeia do Espinhaço in Bahia and Minas Gerais, Brazil, and the Guayana Highland, especially in Venezuela. Although the largest concentration of species is found in the Brazilian center, the largest number of genera (10) is reported from Guayana.

Generic delimitations in the Eriocaulaceae are the subject of some controversy. The bulk of the species are contained in the large genera *Eriocaulon* L., *Paepalanthus* Kunth, *Syngonanthus* Ruhl., and *Leiothrix* Ruhl.; the remaining nine genera together contain only about 35 species. Of the five genera described since Ruhland's classic treatment (1903) (*Carptotepala* Mold., *Comanthera* Lyman B. Smith, *Moldenkeanthus* Morat, *Rondonanthus* Herzog, and *Wurdackia* Mold.), none were described with more than two species, and all but *Moldenkeanthus* of the Madagascar are endemic to the Guayana Highland. (*Moldenkeanthus* has recently been placed by Stützel (1987) in *Paepalanthus*.)

The systematic positions of *Comanthera* and *Carptotepala* have never been adequately investigated in publication, although some workers have informally expressed doubts about their validity (Moldenke, 1968, citing Görts-van Rijn; Giulietti, 1984; Stützel, 1985, in a footnote). Like all genera in the family, they are distinguished on the basis of floral characters, which often prove difficult to interpret in the extremely small flowers. We shall demonstrate here that these monotypic genera are indeed very closely allied with certain sections of *Syngonanthus* and that they lack any specialized characters to adequately distinguish them as genera in their own right.

I. *CARPTOTEPALA*

Moldenke (1951) described the genus *Carptotepala* based on *C. insolita* from Venezuela. Later he transferred *Paepalanthus jenmanii* Gleason, a species of British Guiana, to *Carptotepala* (Moldenke, 1957), and in 1968 he recognized *C. insolita* as a synonym of *C. jenmanii*. He distinguished the genus by the following characteristics: (1) free sepals and petals in both pistillate and staminate flowers; (2) prolongation of the floral

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ANN. MISSOURI BOT. GARD. 78: 460–464. 1991.

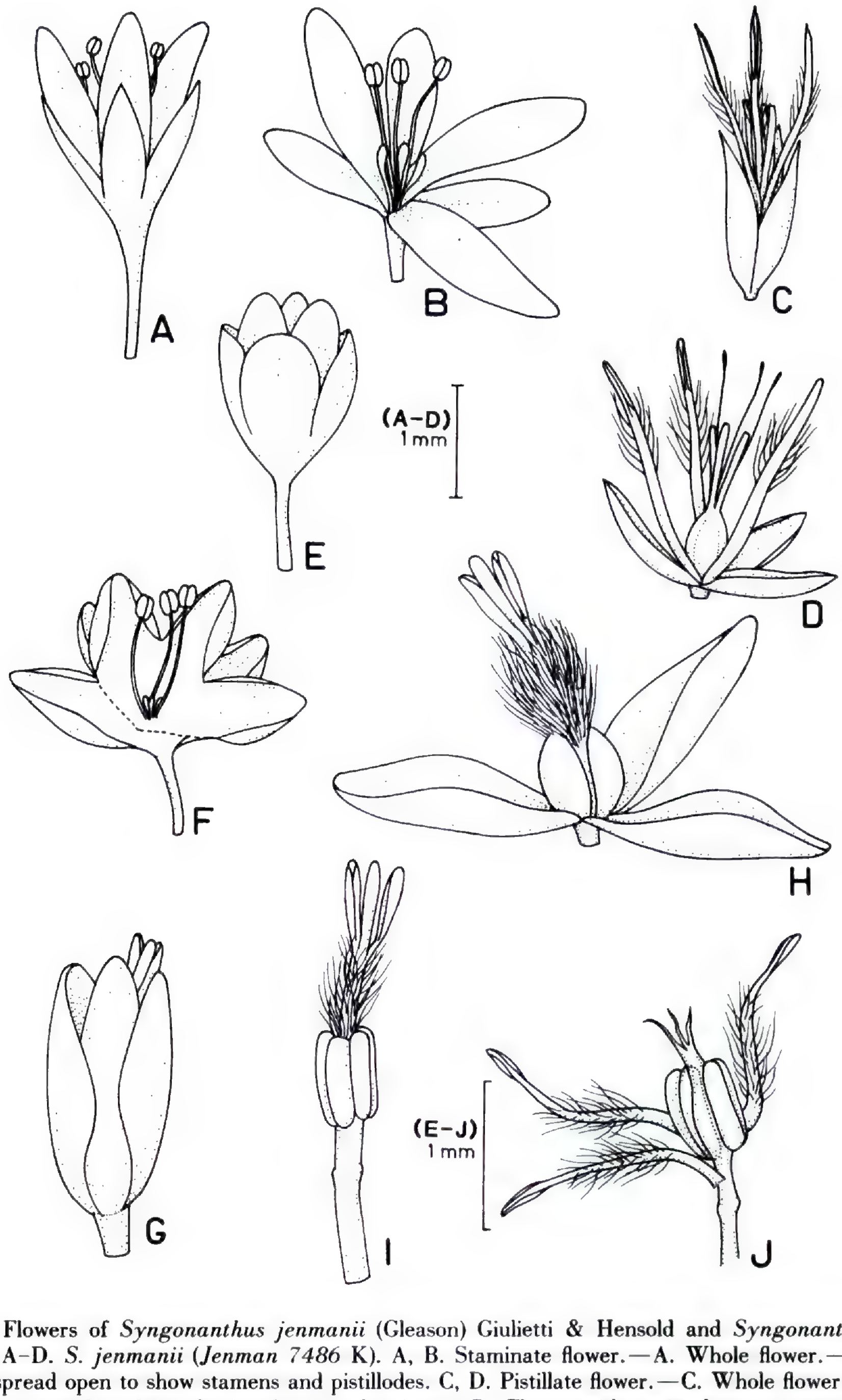

FIGURE 1. Flowers of *Syngonanthus jenmanii* (Gleason) Giulietti & Hensold and *Syngonanthus kegelianus* (Koern.) Ruhl. A–D. *S. jenmanii* (*Jenman 7486* K). A, B. Staminate flower.—A. Whole flower.—B. Flower with perianth parts spread open to show stamens and pistillodes. C, D. Pistillate flower.—C. Whole flower at anthesis, the style tips barely protruding from the involute petal apices.—D. Flower with perianth parts spread open to show gynoecium. E–J. *S. kegelianus* (*Lanjouw & Lindeman 2984* K). E, F. Staminate flower.—E. Whole flower.—F. Flower with perianth dissected open to show stamens and pistillodes. G–J. Pistillate flower.—G. Whole flower.—H. Flower with sepals spread apart, the petals remaining connivent around the style.—I. Flower after release of seeds, the sepals deciduous, the ovary locules open.—J. Same, with the petals dissected away.

receptacle above the calyx in the staminate flowers; and (3) presence of caudate appendages at the tip of the petals in the pistillate flowers.

In fact, the flowers of *C. jenmanii* are extremely similar to those of *Syngonanthus*, especially sects. *Thysanocephalus* (Koern.) Ruhl. and *Eulepis* (Bong.) Ruhl., and may be compared as follows.

In *Carptotepala jenmanii*, the staminate flowers are found at the periphery of the capitulum and are much more abundant than the pistillate,

from which they are easily distinguished by their very long pedicels. These pedicels elevate the staminate flowers above the involucre, as is characteristic of sect. *Thysanocephalus*.

Also as in sect. *Thysanocephalus*, the sepals and petals of the staminate flowers are glabrous, concave, and similar to each other in size and texture (Fig. 1A, B). Contrary to the original descriptions of *C. insolita* and *P. jenmanii*, the sepals are united at the base, and the petals are briefly united or free. Moreover, we did not find elongation of the floral receptacle above the calyx (i.e., an "androphore"), as is known in some *Syngonanthus* (not sects. *Eulepis* or *Thysanocephalus*), and in most *Paepalanthus* and *Eriocaulon*. The description of an androphore in this species may have been due to misinterpretation of the fused basal portion of the corolla.

The pistillate flowers particularly recall sect. *Thysanocephalus*. In these the petals are densely pilose in the middle, and far surpass the sepals, with the glabrous apices curved around and enclosing the style branches. The tips of the style branches protrude slightly beyond the petals, and this apparently was misinterpreted by Moldenke as a "caudate appendage" (Fig. 1C, D).

The sepals and petals appear to be free, though the hairiness of the medial areas of the petals (where fusion normally occurs in *Syngonanthus*) makes it difficult to determine whether the petals are merely cohering about the style or truly fused.

Shallow or ephemeral corolla fusion in both staminate and pistillate flowers is recorded sporadically from sect. *Thysanocephalus*. Staminate flowers with petals nearly free are described for *Syngonanthus squarrosus* Ruhland (1903) and for *S. chrysolepis* Silveira (1928). Pistillate flowers with petals free or united medially are described for *S. flexuosus* Silveira, and petals connate but eventually separating are found in *S. glaber* Silveira (1928).

Moreover, complete loss of petal fusion in staminate and pistillate flower corollas, though rare, is found in *Leiothrix fluitans* (Mart.) Ruhl. and *Rondonanthus* (*Paepalanthus*) *capillaceus* (Klotzsch ex Koern.) Hensold & Giulietti (1991), two species whose closest relatives have the petals fused in at least the staminate flowers. These two species interestingly also share the rheophytic habit with *C. jenmanii*.

Thus, no reliable character remains for isolating this species from *Syngonanthus* sect. *Thysanocephalus*. The relationship is further supported by the characteristic campanulate to urceolate involucre found in *Carptotepala* and sect. *Thysanocephalus*. Inclusion of *Carptotepala jenmanii* within *Syngonanthus* is therefore proposed as follows.

Syngonanthus jenmanii (Gleason) Giulietti & Hensold, comb. nov. *Paepalanthus jenmanii* Gleason, Bull. Torrey Bot. Club 56: 14. 1929. *Carptotepala jenmanii* (Gleason) Mold., Mem. New York Bot. Gard. 9: 278. 1957. TYPE: Guyana. Potaro River, Kaieteur Savanna, *Jenman 1032* (holotype, K).

Carptotepala insolita Mold., Fieldiana, Bot. 28: 114. 1951. TYPE: Venezuela. Bolívar: Rio Karuai, SW base of Ptari-tepui, 1,220 m, *Steyermark 60703* (holotype, NY; isotype, F, GH).

Syngonanthus xeranthemoides var. *grahamae* Mold., Phytologia 8: 395. 1962. TYPE: Guyana. Potaro River, Mahdia goldfield, *V. Graham 154* (holotype, K; isotype, LL). Syn. nov.

Additional specimens examined. VENEZUELA. BOLÍVAR: Canaima, *Trujillo 6021* (MY, VEN); N Gran Sabana, Salto Aponwao, *Huber & Entralgo 7399* (LL); Gran Sabana, Salto Camá, *Davidse 4865* (MO); Ilú-tepui, *Maguire 33516A* (VEN). GUYANA: *Sandwith 1258* (K), *Schomburgk s.n.* (K); Upper Mazaruni River, Kamarang River, base of Utschi Falls, *Tillett & Tillett 45744* (MO); Upper Mazaruni, Kako River, *Tillett & Tillett 45486* (MO); Potaro River, *Abraham 330* (K); Potaro River, Cobanatuk Falls, *Jenman 7486* (K).

The closest affinities of *Syngonanthus jenmanii* appear to lie with the sympatric species *S. xeranthemoides* (C. Martius) Ruhl., which usually occurs on relatively drier sites. *Syngonanthus jenmanii* is distinguished within its section by its occurrence along wet riverbanks, in waterfall spray, and even occasionally with the leaves fully submerged.

II. *COMANTHERA*

Smith (1937) described the genus *Comanthera* to accommodate *C. linderi* Lyman B. Smith. He characterized the new genus by the presence of three distinct types of flowers: (1) the staminate, these pedicellate, with perianth reduced to a vestigial tubular sheath at the base of the flower, and with only one stamen, comose at the apex with long hairs; (2) the pistillate, these sessile, with sepals and petals free; and (3) the sterile, these also pedicellate, with the sepals and petals free.

Moldenke (1966) transferred the species *Syngonanthus kegelianus* (Koern.) Ruhl. to *Comanthera*, without discussion or further descriptive information. Two years later, he recognized *C. linderi* Lyman B. Smith as a synonym of *C. kegeliana* (Koern.) Mold. (1968). He also included in the

synonymy of this species *S. akurimensis* Mold. and *S. akurimensis* var. *amazonicus* Mold.

In the same article, he quoted a letter from A. Görts-van Rijn, who had studied type material of *C. kegeliana*, and questioned the validity of the genus. She compared the appearance of the staminate flowers in Smith's illustration (1937) "with the overripe female flowers, where the fruits have come out and the perianth segments had partly fallen off." Smith's reply in letter was also included, indicating that he was not convinced by her observations.

Because the perianth of eriocaulaceous flowers is chaffy and retains its form and color long after anthesis, differences between flowers at different stages may easily be misinterpreted as taxonomic differences. Therefore, flowers were examined from capitula of *C. kegeliana* in various stages of maturation. Only two types of flowers were observed, staminate and pistillate. At anthesis, these possess the following organization:

Staminate flower. Long-pedicellate; sepals three, free, glabrous; petals three, connate briefly at base, glabrous, somewhat surpassing the sepals; stamens three, the filaments filiform, included, anthers dithecous; pistillodes very small (Fig. 1E, F).

Pistillate flower. Short-pedicellate; sepals similar to those of staminate flowers; petals somewhat surpassing the sepals, connate and long-pilose medially, but separating very easily, free at apex and base, the apical portion somewhat broader than the medial portion and with the lateral margins involute, enclosing the styles; gynoecium with a three-locular ovary, and three elongate simple style branches slightly surpassing the petals (Fig. 1G, H).

The old flowers persist for some time in the head and present the following organization:

Staminate flower. Same as above, but the anthers lost and the filaments delicate and filiform.

Pistillate flower. After fertilization, the pedicels elongate considerably to equal those of the staminate flowers. A loculicidal capsule is formed with a membranaceous pericarp. After the liberation of the seed the two valves of each locule recurve toward the floral axis, completely enclosing the narrow bases of the petals. At the same time, the sepals fall, leaving only the pedicel and a small ring of tissue representing the scar where the sepals were inserted.

It is evident that the sterile, long-pedicellate flower portrayed in Smith's (1937) description and figures (pl. 2, fig. 59) is in reality a staminate flower that has lost its anthers after anthesis.

The pistillate flower described and illustrated is in all respects like that of the material examined, except that the petals are depicted as free instead of connate medially. However, in dissection of pistillate flowers of this species it is quite easy to separate the pilose membranous petals without awareness of doing so. Smith described the flowers as sessile, but as noted, they are very short-pedicellate before fertilization, and may appear sessile in comparison to later stages of development. Moreover, truly sessile flowers are virtually unknown in Eriocaulaceae.

The staminate flower described and illustrated as possessing a single stamen comose at the apex is identical in appearance to the female flower after liberation of the seeds, as Görts-van Rijn suggested. The abscission scar left by the sepals corresponds to the reduced perianth described by Smith; the single dithecous anther corresponds to the two visible ovary locules with the pericarp completely recurved toward the center of the flower (the third locule is of course not evident as the flower is viewed from the side); and the comose apex of the "anther" corresponds to the narrow pilose segments of the petals, which project above the ovary, their bases hidden by the recurved locule walls.

The floral structure of *Comanthera kegeliana* and the variations found in progression from bud to fruiting are characteristic for the majority of species of the genus *Syngonanthus*, especially those of sect. *Eulepis*, in which *S. kegelianus* was first described.

It is therefore proposed that the genus *Comanthera* be synonymized with the genus *Syngonanthus* and its single species be placed in sect. *Eulepis*.

Syngonanthus kegelianus (Koern.) Ruhl., Pflanzenr. IV. 30: 273. 1903. *Paepalanthus kegelianus* Koern. in C. Martius, Fl. Bras. 33(1): 438. 1863. *Dupatya kegeliana* (Koern.) Kuntze, Revis. gen. pl. 2: 746. 1891. *Comanthera kegeliana* (Koern.) Mold., Phytologia 13: 218. 1966. TYPE: Surinam, Mariepaston, *Kegel 1473* (holotype, GOET not seen, photo, K; isotype fragment, B not seen).

Comanthera linderi Lyman B. Smith, Contr. Gray Herb. 117: 38, pl. 2. 1937. TYPE: Guyana, Rockstone, *Linder 40* (holotype, GH not seen; isotype, NY).

Syngonanthus akurimensis Mold., Phytologia 2: 371. 1947. TYPE: Venezuela. Bolívar: Cerro Akurimá, *Tamayo 3234* (holotype, US not seen; isotype, NY). Syn. nov.

Additional material examined. VENEZUELA. BOLÍVAR: *Lockhart s.n.* (K); along Río Uairén, *Lasser 1705* (F, VEN). GUYANA. Georgetown, Atkinson Field, *Maas & Westra 3571* (K), *McKee 10681* (K), *Robertson & Austin 268* (NY); Rockstone, *Gleason 652* (NY). SURINAM. Jodensavanne, *Lanjouw & Lindeman 2984* (K).

Syngonanthus kegelianus is readily identified even from descriptions and photos because of the distinct pubescence on the leaves and peduncle sheaths of this species, i.e., stiff, erect hairs on leaf undersurface and appressed white malpighian scales on upper leaf surface and on peduncle sheaths. It is the only member of *Syngonanthus* sect. *Eulepis* found in the Guayana Highlands, and is fairly unusual within its section due to the small, hyaline, relatively unspecialized upper involucral bracts.

It has very close affinities with *Syngonanthus ulei* Ruhl. of Amazonian Brazil, which is only readily distinguished by the long spreading hairs on leaves and sheaths and the lack of white scalelike malpighian hairs. It may represent only a variety of *S. kegelianus*.

Syngonanthus akurimensis var. *amazonicus* Mold. (Phytologia 3: 42. 1948), which Moldenke considered synonymous with *S. kegelianus*, is probably identical with *S. ulei*, as is *S. kuhlmannii* f. *viviparus* Mold. (Phytologia 37: 97. 1977).

These new additions to the generic synonymy of *Syngonanthus* are summarized as follows:

Syngonanthus Ruhl. in Urban, Symb. Antill. 1: 487. 1900. TYPE: *Syngonanthus umbellatus* (Lam.) Ruhl. (*Eriocaulon umbellatum* Lam.).

Carptotepala Mold., Fieldiana, Bot. 28: 114. 1951. TYPE: *Carptotepala insolita* Mold.

Comanthera Lyman B. Smith, Contr. Gray Herb. 117: 38. 1937. TYPE: *Comanthera linderi* Lyman B. Smith.

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STUDIES IN NEOTROPICAL PALEOBOTANY. X. THE PLIOCENE COMMUNITIES OF PANAMA—COMPOSITION, NUMERICAL REPRESENTATIONS, AND PALEOCOMMUNITY PALEOENVIRONMENTAL RECONSTRUCTIONS[1]

Alan Graham[2]

Abstract

The middle Pliocene Gatun Formation of central Panama consists of carbonaceous sandstones and siltstones preserving a pollen and spore flora of 110 recognized types. The most abundant are *Operculodinium* and *Spiniferites* (dinoflagellates), *Alsophila*, *Pteris*, monolete fern spores, Gramineae, Palmae, *Casimiroa*, *Combretum/Terminalia*, *Eugenia/Myrcia*, *Faramea*, *Ilex*, Malpighiaceae, and *Rhizophora*. These sort into 11 principal paleocommunities: shallow water marine community, mangrove swamp, floating/submerged fresh water aquatic community, lowland fresh water marsh community and fringing vegetation, and tropical wet, tropical moist, premontane wet, premontane moist, premontane rain, lower montane moist, and tropical dry forests. The primary differences between the middle Pliocene Gatun communities and older Eocene and lower Miocene vegetation are (1) increased biotic diversity, (2) the first appearance of substantial quantities of grass pollen (maximum 7.5%), (3) a more fully developed and extensive tropical dry forest, (4) increased physiographic diversity, (5) better representation of lower montane forests, and (6) possibly, the first indication of developing wetter Atlantic and drier Pacific provinces in southern Central America.

An assemblage of 110 fossil pollen and spores, including 13 with no previously known fossil record and 27 unknowns, has been recovered from the middle Pliocene Gatun Formation of central Panama. The systematics of the Gatun flora has been presented earlier (Graham, 1990, 1991a, b), and the geology is summarized in Graham et al. (1985). This paper concludes the study with presentation of the composition, numerical representations, and paleocommunity/paleoenvironmental reconstructions.

Materials and Methods

Extraction, slide preparation, and photographic techniques are discussed in Graham (1985). Terminology for vegetation types follows Holdridge (1947; Holdridge et al., 1971), and distributions and community assignments are based on Croat (1978) and D'Arcy (1987). Depths along the core are given in feet, following the original log data.

Composition and Numerical Representations

The composition, distribution, and percentage for each palynomorph at the nine levels along the Gatun core are given in Table 1. The distribution of the 15 most abundant microfossils (2% or greater from at least one level) is presented in Figure 1.

Sediments in the lower portions of the profile (257.0–253.0′) consist of fine- to medium-grained sandstone with interspersed lenses of coalified lignite. The sandstone suggests near-shore deposition as rivers and surface waters slow and drop heavier mineral particles first upon entering the ocean. The environmental setting was paralic (marine coastal), tropical to warm-temperate (presence of *Rhizophora*), estuarine (bay), and low-energy where autochthonous organic material accumulates rather than being dispersed by coastal currents. Percentages of *Rhizophora* pollen are relatively low (3.0%, 2.5%, 5.0%; Fig. 1). The lower portion of the core

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TABLE 1. Identification and numerical representation of fossil palynomorphs from the Gatun Formation, Panama. Percentages are based on counts of 200 from slide 1 of each sample. (—) indicates specimen not encountered in tabulation.

Species	Depth (feet)								
	257.0	255.5	253.0	250.0	223.5	223.0	222.5	178.0	162.0
Pyrrophyta	—	—	—	—	7.5	7.0	7.5	—	—
Lycopodiaceae									
Lycopodium									
type 1	—	—	—	—	1.0	—	—	—	—
type 2	—	—	—	—	—	—	—	—	—
type 3	—	—	—	—	1.5	—	—	—	—
type 4	—	—	—	0.5	—	—	—	—	—
Selaginellaceae									
Selaginella	—	—	—	—	1.5	—	—	—	—
Cyatheaceae									
Alsophila	3.5	—	3.5	—	6.0	8.0	8.0	3.0	9.0
Cnemidaria	1.5	—	0.5	—	—	—	—	1.5	—
Cyathea									
type 1	—	—	1.5	—	1.5	1.5	—	1.5	1.5
type 2	—	—	—	—	—	—	—	—	—
Ophioglossaceae									
Ophioglossum	—	—	—	—	—	—	—	—	—
Polypodiaceae									
Grammitis	—	—	—	—	1.0	—	—	—	—
Pteridaceae									
Ceratopteris	—	—	—	—	1.0	1.5	—	1.5	1.5
Pteris									
type 1	—	—	—	—	—	—	—	—	—
type 2	—	—	—	—	—	—	—	—	—
type 3	—	—	—	—	—	—	—	—	—
type 4	—	—	—	0.5	3.5	7.0	8.5	8.5	10.0
type 5	—	—	—	—	—	—	—	—	—
Trilete fern spore									
type 1	0.5	0.5	—	—	—	—	—	—	—
type 2	—	—	—	—	—	—	—	—	—
Dryopteridaceae									
Ctenitis									
type 1	1.5	0.5	1.0	—	—	1.0	—	1.5	—
type 2	—	—	—	—	—	—	—	—	—
type 3	—	—	—	—	—	—	—	—	—
Monolete fern spore									
type 1	14.0	8.5	8.0	1.5	9.0	14.0	13.0	14.0	26.0
type 2	7.0	13.5	9.5	3.0	11.5	8.5	4.5	24.0	16.0
type 3	—	—	—	—	—	—	—	—	1.0
type 4	—	—	—	—	—	—	—	—	—
type 5	—	—	—	—	—	—	—	—	—
Podocarpaceae									
Podocarpus	1.0	1.0	—	—	—	—	—	—	—
Gramineae	7.5	6.5	4.5	—	—	1.0	—	—	—

TABLE 1. Continued.

Species	Depth (feet)								
	257.0	255.5	253.0	250.0	223.5	223.0	222.5	178.0	162.0
Palmae									
type 1	12.5	20.0	6.0	3.5	12.0	18.0	20.0	13.0	6.0
type 2	7.0	12.0	4.5	1.0	3.5	0.5	1.5	1.5	—
Annonaceae									
Cymbopetalum	—	—	—	—	—	—	—	—	—
Aquifoliaceae									
Ilex	2.5	2.0	3.0	1.0	3.5	—	4.5	2.5	3.5
Bombacaceae									
cf. *Aguiaria*	—	—	—	—	1.0	1.0	1.5	—	—
Bernoullia	—	—	—	—	—	—	—	—	—
Ceiba	—	—	—	—	—	—	—	—	—
Pseudobombax	—	—	—	1.5	—	0.5	—	—	—
Burseraceae									
Bursera	—	—	—	—	—	—	—	—	—
Cabombaceae									
Cabomba	—	—	—	—	—	—	—	—	—
Combretaceae									
cf. *Bucida*		—	—	—	—	—	—	—	—
Combretum/Terminalia	4.5	6.5	—	—	—	—	—	—	—
Compositae									
Mutisieae type	—	—	—	—	—	—	—	—	—
Cucurbitaceae									
cf. *Cionosicys*	—	—	—	—	—	—	—	—	—
Ericaceae									
type 1	—	—	0.5	—	—	—	—	1.0	—
type 2	—	—	—	—	—	—	—	—	—
Euphorbiaceae									
Alchornea	—	—	—	—	—	—	—	—	—
cf. *Glycydendrum*	1.0	—	2.0	1.0	—	1.5	2.0	—	—
cf. *Jatropha*	—	—	—	—	—	—	—	—	0.5
cf. *Stillingia*	—	—	—	—	—	—	—	—	—
Fagaceae									
Quercus	—	—	—	—	—	—	—	—	—
Juglandaceae									
Alfaroa/Oreomunnea	—	—	—	—	—	—	—	—	—
Leguminosae									
Mimosoideae									
Acacia	—	—	—	—	—	—	—	—	—
Caesalpinioideae									
Crudia	0.5	0.5	—	—	—	—	—	0.5	—
Papilionoideae									
Erythrina	—	—	—	—	—	—	—	—	—
Lentibulariaceae									
Utricularia	—	—	—	—	—	—	—	—	—

TABLE 1. Continued.

Species	Depth (feet)								
	257.0	255.5	253.0	250.0	223.5	223.0	222.5	178.0	162.0
Loranthaceae									
type 1	—	—	—	—	—	—	—	—	—
type 2	—	—	—	—	—	—	—	—	—
Malpighiaceae									
type 1	—	—	2.5	—	—	—	—	7.0	—
type 2	—	—	—	—	—	—	—	—	—
Malvaceae									
Hampea/Hibiscus	—	0.5	0.5	1.5	—	—	1.5	—	—
Melastomataceae	—	—	—	—	—	—	—	—	—
Meliaceae									
Cedrela	—	—	—	—	—	—	—	—	—
Guarea	0.5	—	—	—	—	—	—	—	—
Myrtaceae									
Eugenia/Myrcia	6.5	5.0	8.0	1.0	2.5	—	—	—	—
Nymphaeaceae (see Cabombaceae)									
Onagraceae									
Hauya	—	—	—	—	—	—	—	—	1.5
Rhizophoraceae									
Rhizophora	3.0	2.5	5.0	82.0	9.5	10.0	9.0	8.0	7.5
Rubiaceae									
Chomelia type	—	1.0	—	—	—	1.0	—	—	—
Cosmibuena	—	0.5	—	—	—	—	—	1.0	—
Faramea									
type 1	2.5	—	1.0	—	—	—	2.0	—	1.5
type 2	—	—	—	—	—	—	—	—	—
Posoqueria	—	—	—	—	—	—	—	—	—
Rutaceae									
Casimiroa	1.5	—	3.5	—	—	—	2.0	—	—
Sapindaceae									
Allophylus	—	—	—	—	—	—	—	—	—
Cupania	—	—	—	—	0.5	—	—	—	—
Paullinia	—	—	—	—	—	—	—	—	—
Serjania	—	—	—	—	—	—	—	—	—
Sapotaceae									
cf. *Bumelia*	0.5	0.5	0.5	0.5	—	—	—	—	—
Symplocaceae									
Symplocos	—	—	—	—	—	—	—	—	—
Tiliaceae									
Mortoniodendron	1.0	—	—	—	—	—	—	—	—
Verbenaceae									
Aegiphila	—	—	—	—	—	—	—	—	—
Petrea	—	—	—	—	—	—	—	—	—

TABLE 1. Continued.

Species	Depth (feet)								
	257.0	255.5	253.0	250.0	223.5	223.0	222.5	178.0	162.0
Unknown									
1	—	0.5	3.5	—	—	1.5	—	1.0	—
2	—	—	2.5	—	—	—	—	—	—
3	—	—		—	—	—	—	—	—
4	2.5	5.0	1.5	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—	—
6	1.5	—	—	—	2.0	—	—	—	—
7	1.5	—	3.0	—	—	0.5	—	—	—
8	—	0.5	—	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	—
10	—	—	—	—	—	—	—	—	—
11	—	—	—	—	—	—	—	—	—
12	—	0.5	—	—	—	—	—	—	—
13	—	—	—	—	1.0	—	—	—	—
14	—	—	2.5	—	—	—	—	—	—
15	—	0.5	—	—	—	—	—	—	—
16	—	0.5	—	—	—	—	—	—	—
17	—	—	—	0.5	—	—	2.0	—	—
18	—	—	0.5	—	—	—	—	—	—
19	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—
21	—	—	—	—	—	0.5	—	—	—
22	—	—	0.5	—	1.0	0.5	—	—	—
23	—	—	—	—	—	—	—	—	—
24	—	0.5	2.5	—	5.0	4.5	3.5	—	4.0
25	—	—	3.0	—	—	—	—	—	—
26	—	—	3.0	—	—	—	—	—	—
27	2.0	1.5	2.0	0.5	1.5	—	—	1.0	—
Other unknowns	12.5	9.0	10.0	0.5	12.0	10.5	9.0	8.0	10.5

is characterized by high percentages of monolete fern spores (combined values 21%, 22%, 17.5%) and palm pollen (19.5%, 32%; Table 1), and relatively high percentages of grass pollen (7.5%, 6.5%, 4.5%). The figures for grass pollen are significant when compared to values for older floras from the same region. Maximum percentages for grass pollen in the middle(?) to upper Eocene Gatuncillo and the lower Miocene Culebra, Cucaracha, and La Boca floras of central Panama, and the Uscari sequence flora of Costa Rica (Graham, 1985, 1988a, b, 1989a, 1987a) are 0%, 1%, 0%, less than 1%, and 0%, respectively. The appearance of comparatively large amounts of grass pollen in the middle Pliocene Gatun flora is one of the principal differences between it and older Tertiary floras from the same region.

At level 250′ a major change in microfossil percentages occurs, with *Rhizophora* pollen reaching 82% of the total flora. This compares to previous values of 3.0%, 2.5%, and 5% at levels 257.0, 255.5, and 253.0′, respectively (Table 1, Fig. 1). All other major pollen and spore types decrease in value (Fig. 1), or disappear completely. Only 16 palynomorph types (14%) were encountered at level 250′, compared to 48 types (44%) for the preceeding three levels. Monolete fern spores decrease from combined values of 21%, 22%, and 17.5% to 4.5%, and palm pollen decrease from 19.5%, 32%, and 10.5% in the three lowest levels to 4.5% at level 250.0′.

A change in sediment type, and in the microfossil assemblage, occurs at levels 223.5–222.5′. The sediment particle size changes from a fine- to medium-grained sandstone with lenses of lignite, to a finer siltstone with organic matter dispersed through the sediment. Smaller-grained particles remain suspended longer upon entering the ocean and are characteristic of sedimentation further from the shore where currents disperse the microscopic-size organic component. The principal change in the microfossil flora at levels 223.5–222.5′ is the first

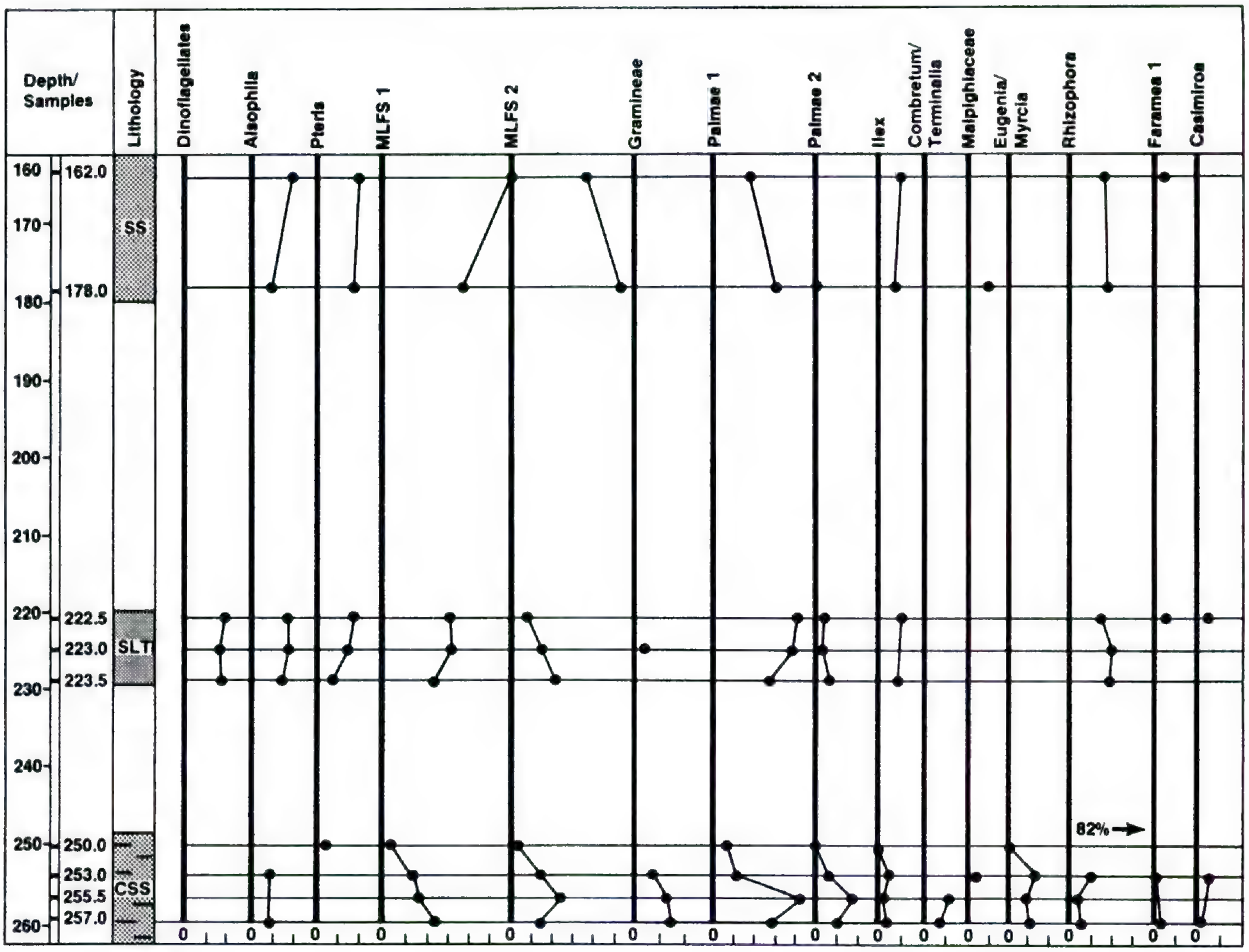

FIGURE 1. Vertical distribution of the most common palynomorphs at nine levels along a core through the middle Pliocene Gatun Formation, Republic of Panama. CSS = carbonaceous sandstone (dark lines indicate lenses of lignite), SLT = siltstone, SS = sandstone. Each mark on the bottom scale represents 5%.

appearance of the shallow water marine dinoflagellates *Operculodinium* and *Spiniferites* (Graham, 1989a, p. 51, figs. 2–4). Diversity of palynomorphs decreases from 44% at levels 257.0–253.0′, to 32% at levels 223.5–222.5′ (Fig. 1), and many are represented by thick-walled fern spores (*Alsophila*, *Pteris* type 4, monolete fern spore types 1, 2) and pollen (*Ilex*) that can withstand long-distance transport, or by wind-dispersed pollen produced in large quantities that can readily be blown into depositional basins (Palmae type 1; Table 1).

The upper two levels of the Gatun core (178, 162′) consist of medium-grained sandstone with dispersed organic material. Preservation of the palynomorphs is only fair, diversity is low (21%), and almost all palynomorphs are represented by thick-walled forms (fern spores, *Ilex*, Malpighiaceae) or forms belonging to anemophilous species (Palmae type 1).

Collectively, the lithology and composition of the Gatun flora reveals a dynamic landscape with frequent and significant changes in the physical environment. Sedimentation began in a near-shore setting close to the source area for the palynomorphs (257.0–250.0′). The site was subsequently inundated by marine waters, reflected first by an increase in *Rhizophora* pollen (250.0′), and then by the presence of *Operculodinium* and *Spiniferites* (223.5–222.5′). The sediments and microfossil composition of the uppermost levels (178.0, 162.0′) suggest uplift of the adjacent land with steeper gradients carrying coarser-grained sandstone out over the site. Lignitic lenses could not accumulate in this high-energy environment, and plant microfossils are represented by thick-walled, resistant spores and pollen (drift specimens), and by wind-dispersed pollen. Similar cycles of deposition are repeated throughout the Gatun core, and are also evident in many other Tertiary formations in this tectonically active region. The genesis of these numerous, short-term cycles was likely relatively rapid uplift and subsidence of the land, superimposed on a general eustatic rise in sea level, which

continued until about the mid-Pliocene, when levels dropped, reflecting the early stages of extensive polar glaciation (see illustration in Graham, 1987b, fig. 4). Intense tectonic activity is clearly evident in the structural geology of central Panama (Graham et al., 1985, fig. 2, p. 49, Culebra Formation; Lowrie et al., 1982, fig. 3).

The changing position of the source area vegetation relative to the Gatun core site is reflected in the diversity values noted earlier. These values (viz., percent of the total flora of 110 palynomorphs represented at each of the three groups of levels; Fig. 1) show a trend through the profile. The figures are very general, and a number of factors influence the quantitative and qualitative representation of plant microfossils in a depositional basin (e.g., distance of the basin from the source area, sediment type, rate of sedimentation, amount of sediment in each sample, number of samples for each level). Nonetheless, a decrease in diversity and an increase in thick-walled spores and pollen, and anemophilous pollen types, is evident from the bottom to the top of the Gatun core. Levels 257.0, 255.5, and 253.0′ (representing 4′ of sediment), with the site of deposition closest to the source area vegetation, contain 44% of the Gatun palynomorph types. Levels 223.5, 223.0, and 222.5′ (representing 1′ of sediment), and further removed from the source area, contain 32% of the palynomorph types. Levels 178.0 and 162.0′ (16′ of sediment) contain 21%, with poorer preservation and evidence of differential preservation (thick-walled pollen/spore types). Levels 257.0–253.0′ are most representative of the vegetation growing in the region during Gatun time.

The 110 palynomorphs recognized for the Gatun flora are considerably more than has been recorded from the preceeding early Miocene floras in southern Central America: Culebra—55 taxa; Cucaracha—21 taxa; La Boca—54 taxa; Uscari—44 taxa.

One of the principal differences between the Gatun assemblage and older Tertiary floras from the same region is the marked increase in the kinds of palynomorphs present, reflecting greater diversity in the developing southern Central American vegetation.

Paleocommunities

Some of the 110 taxa recognized from the Gatun microfossil flora indicate the presence of a specific paleocommunity (e.g., *Rhizophora*). Others are *suggestive* of a particular community (e.g., *Podocarpus*), especially when common associates of that community are also present (e.g., *Alfaroa/Oreomunnea*, *Quercus*), even though these may extend into adjacent communities along transition zones, or occur as edaphically or physiographically controlled local outliers in different communities. Other taxa range widely through several community types (e.g., *Lycopodium*).

Most pollen and spore types in the Gatun assemblage can be identified only to genus, and many of the larger modern genera contain species that grow under widely different ecological conditions. For example, *Quercus oleoides* Cham. & Schldl. is a lowland tropical species, while *Q. aaata* Muller, *Q. brenesii* Trel., *Q. copeyensis* Muller, and others grow at higher altitudes in temperate habitats. Other pollen and spores can be identified only to genus or above (e.g., monolete fern spore types 1–5, Gramineae, Palmae, Ericaceae, Malpighiaceae, Melastomataceae). Unknown types 1–27 could represent taxa from any number of communities, while the pollen of some important tropical families (e.g., Lauraceae) does not preserve in the fossil record.

For these and other reasons, paleocommunity reconstructions based on palynological data alone are tentative, and provide only a general picture of the paleovegetation. The probability of some version of a modern community being represented in a fossil assemblage is enhanced, however, in descending order of importance, by the presence of (1) elements restricted to a particular community, (2) elements typical of a community, even though they may range into other vegetation types, (3) a combination of several genera that, even though individually widespread, are collectively typical of a given community, and (4) a very large number of genera that occur in a particular community even though none are restricted to, or even typical of, that particular vegetation (e.g., numerical abundance). Once a tentative model of paleocommunity types has been established, it can be assessed in terms of (1) paleophysiographic and paleoclimatic reconstructions based on other lines of evidence (e.g., paleotemperature curves, fossil vertebrate faunas), (2) plate tectonic data (viz., land–sea relationships), (3) biogeographic data on the timing and direction of migrations, and geographic affinities, derived from studies of the past (fossil occurrences) and present distribution of other taxa, (4) consistency with results from studies of other fossil floras of the same age from the same region, and (5) consistency with trends and patterns established from studies of older and younger biotas and from the above collective evidence.

Taxa identified from the Gatun flora are ar-

TABLE 2. Distribution of taxa identified from the middle Pliocene Gatun Formation among comparable community types in Panama. Placement is according to principal or most common occurrence(s), and most range through more than one community.

Shallow Water Marine Community
Operculodinium, Spiniferites
Mangrove Swamp
Hibiscus, Rhizophora
Floating/Submerged Fresh Water Aquatic Community
Ceratopteris, Utricularia, Cabomba
Lowland Fresh Water Marsh Community and Fringing Vegetation
Monolete fern spore types 1–2 (likely representing Blechnaceae, Polypodiaceae, Pteridaceae), Palmae type 1, *Bucida*
Tropical Wet Forest (31 taxa)
Lycopodium, Selaginella, Cnemidaria, Ctenitis, Pteris, Aegiphila, cf. *Aguiaria, Alchornea, Allophylus, Bernoullia, Bucida, Bursera, Chomelia, Combretum, Crudia, Cupania, Cymbopetalum, Erythrina, Eugenia/Myrcia, Faramea,* cf. *Glycydendrum, Guarea, Hampea/Hibiscus, Mortoniodendron, Paullinia, Petrea, Posoqueria, Pseudobombax,* cf. *Stillingia, Symplocos, Terminalia*
Tropical Moist Forest (38 taxa)
Lycopodium, Selaginella, Alsophila, Cnemidaria, Cyathea, Ophioglossum, Pteris, Aegiphila, cf. *Aguiaria, Acacia, Alchornea, Allophylus, Bernoullia, Bursera, Cedrela, Ceiba, Chomelia,* cf. *Cionosicys, Combretum/Terminalia, Cosmibuena, Crudia, Cupania, Cymbopetalum, Erythrina, Eugenia/Myrcia, Faramea, Guarea, Hampea,* cf. *Jatropha, Mortoniodendron, Paullinia, Petrea, Posoqueria, Pseudobombax, Quercus, Serjania* cf. *Stillingia, Symplocos*
Premontane Wet Forest (27 taxa)
Lycopodium, Selaginella, Alsophila, Cnemidaria, Ctenitis, Cyathea, Pteris, Aegiphila, Alchornea, Allophylus, Bernoullia, Cedrela, Combretum/Terminalia, Cosmibuena, Crudia, Cupania, Cymbopetalum, Erythrina, Eugenia/Myrcia, Faramea, Hampea, Petrea, Paullinia, Posoqueria, Serjania, cf. *Stillingia, Symplocos*
Premontane Moist Forest (21 taxa)
Ophioglossum, Alfaroa/Oreomunnea, Aegiphila, Allophylus, Bursera, Ceiba, cf. *Cionosicys, Combretum/Terminalia, Eugenia, Faramea, Hampea, Hauya, Ilex, Paullinia, Petrea, Posoqueria, Pseudobombax, Quercus, Serjania,* cf. *Stillingia, Symplocos*
Premontane Rainforest (11 taxa)
Alchornea, Bernoullia, Cosmibuena, Cymbopetalum, Erythrina, Hampea, Paullinia, Petrea, Serjania, cf. *Stillingia, Symplocos*
Lower Montane Moist Forest (12 taxa)
Lycopodium, Selaginella, Alsophila, Cyathea, Grammitis, Ophioglossum, Pteris, Podocarpus, Acacia, Alfaroa/Oreomunnea, Ilex, Quercus
Tropical Dry Forest (11 taxa)
Gramineae, *Acacia, Allophylus, Bursera, Cedrela, Ceiba, Combretum,* cf. *Jatropha, Posoqueria, Pseudobombax, Serjania*
Lower Montane Wet Forest (6 taxa)
Lycopodium, Selaginella, Alsophila, Ctenitis, Cyathea, Pteris,
Premontane Dry Forest (6 taxa)
Gramineae, *Acacia, Bursera, Combreatum, Eugenia,* cf. *Jatropha*
Montane Moist Forest (4 taxa)
Grammitis, Podocarpus, Alfaroa, Quercus
Montane Wet Forest (3 taxa)
Cnemidaria, Cyathea, Grammitis
Lower Montane Rainforest—none
Montane Rainforest—none

ranged into paleocommunities in Table 2, based on the occurrence of their presumed modern analogs. The Gatun Formation is primarily a shallow water marine deposit (Graham, 1991a, fig. 1), with all terrestrial pollen-bearing material coming from subsurface well cores. A shallow water marine community, and a coastal, warm-temperate to tropical depositional environment, are indicated by the dinoflagellates *Operculodinium* and *Spiniferites.* Fringing the coast was a mangrove swamp (*Rhizophora*), with the pollen form *Hampea/Hibiscus* likely representing *Hibiscus tiliaceous* L./*H. sororius* L.f., tropical beach plants. A floating/submerged fresh water aquatic community, beyond the influence of marine or brackish waters, is suggested by microfossils of *Ceratopteris, Cabomba,* and *Utricularia.* Also in the lowlands and not influenced by marine waters were marsh or wet-habitat communities reflected by non-tree fern spores (maximum 26%, Table 1) of the Blechnaceae, Polypodiaceae, Pteridaceae type. Some palm pollen (maximum 20%) probably represents species associated with or bordering the marsh community. *Bucida* is a small tree or shrub occurring in strand thickets and wet forests at elevations from sea level to about 1,000 m.

It is difficult to distinguish between the various lowland forest types on the basis of palynological evidence because the generic composition of these forests is often similar, and transition zones may be broad and gradual. The tropical moist forest is represented by 38 taxa that can occur in that formation, the tropical wet forest by 31 taxa, the premontane wet forest by 27 taxa, and the premontane moist forest by 21 taxa (Table 2). It is

likely that some form of all of these communities were represented in the middle Pliocene vegetation of central Panama. The premontane rainforest (11 taxa), lower montane moist forest (12 taxa), and tropical dry forest (11 taxa) are also represented by a number of taxa and/or by elements characteristic of these vegetation types. For example, the association of *Podocarpus*, *Alfaroa/Oreomunea*, *Ilex*, and *Quercus* is most typical of the lower montane moist forest. The presence of pollen of 11 taxa that can or typically do occur in the tropical dry forest compares with the following figures from other Tertiary floras in the region:

Gatuncillo (middle(?) to lower Eocene, Panama)—4 (+ two widespread)
Culebra (lower Miocene, Panama)—7
Cucaracha (lower Miocene, Panama)—0
La Boca (lower Miocene, Panama)—0
Uscari (lower Miocene, Costa Rica)—0

Grass pollen, virtually absent from these older floras, increases to values of 7.5%, 6.5%, and 4.5% in the Gatun flora (Table 1). Many of the Gramineae were probably associated with the tropical dry forest. One of the principal differences between the older Tertiary floras of southern Central America, and the Gatun flora, is the initial appearance of a more fully developed and widespread tropical dry forest in the middle Pliocene. In turn, this suggests that relatively extensive, sustained, and adequate food resources for moderate- to larger-sized herds of browsing and grazing mammals, migrating in substantial kinds and numbers between North and South America near the end of the Pliocene (ca. 2.4 myr), began to appear in the middle Pliocene. Prior to that time, smaller numbers of browsers and grazers were probably supported by shifting, temporal, seral communities developing in response to intense tectonic and volcanic activity, documented for southern Central America during the Tertiary (Graham, 1988b, pp. 1476–1478).

Paleophysiography

Estimates of maximum altitudes in proto-Central America must be general because of the wide altitudinal range of many genera, and because montane species are underrepresented in sediments accumulating in lowland basins of deposition. However, Muller (1959) has shown that pollen from upland communities is commonly transported into coastal environments by rivers, and Germeraad et al. (1968) believe that outwashing by surface runoff is an important means of pollen transport in the tropics. This accounts, in part, for the better representation of both entomophilous pollen types (e.g., *Cymbopetalum*, cf. *Cionosicys*, *Acacia*, *Erythrina*, *Hampea/Hibiscus*, *Hauya*) and pollen from montane species in tropical assemblages than in temperate microfossil floras. Thick-walled spores and pollen (e.g., *Gramminitis*) and wind-dispersed types (*Podocarpus*) from inland and upland habitats are readily incorporated into coastal deposits. Thus, montane communities may be underrepresented, but not a priori absent from estuarine sediments.

The impression from the Gatun assemblage is that low to moderate montane habitats are better represented than in Eocene and lower Miocene floras from the same region. *Gramminitis*, *Podocarpus*, and *Alfaroa/Oreomunnea* are all low- to mid-elevation montane plants in southern Central America, and they occur together for the first time in the Gatun flora. Also, the number of genera that can occur in the lower montane moist forest is greater in the Gatun flora (12 genera) than in the Gatuncillo (3) or Culebra (6) floras.

Pollen assemblages from older Tertiary floras in southern Central America (Graham, 1987b, 1988c, d) indicate that all components could be accommodated within elevations ranging from sea level to about 1,400 m (Graham, 1989b). The Gatun flora suggests slightly higher elevations, to an estimated 1,700 m, within pollen rain deposition of the Gatun site. Current maximum elevations are 3,820 m (Cerro Chirripó) and 3,432 m (Volcán Irazú) in Costa Rica, and 3,475 m (Volcán Barú) in Panama, all to the west of the Gatun locality. The middle Pliocene Gatun flora provides the first evidence for low to moderate montane habitats in southern Central America.

A more extensive landscape and increased physiographic diversity accounts, in part, for the larger number of genera in the Gatun flora (110) than in other Tertiary floras from southern Central America (e.g., 55 taxa in the Culebra flora; 21 in the Cucaracha). These, in turn, sort into a greater number of paleocommunities which are better represented in the Gatun assemblage (e.g., the lower montane moist forest; tropical dry forest). In particular, the tropical dry forest may reflect the beginning of a differentiation into drier (Pacific) and wetter (Atlantic) zones in southern Central America.

Paleoclimate

Climates of the middle Pliocene in southern Central America must have been similar to those of the present because all taxa identified from the Gatun Formation, with the exception of *Crudia*

and possibly some cf. identifications, grow in the area today. An approximation of these climates may be gained by considering those on nearby Barro Colorado Island. There the annual rainfall ranges from 190 to 360 cm (76 to 143 inches), and averages 275 cm (107.3 inches). "The climate is markedly seasonal, with a sharp dry season usually starting in mid-December and continuing until about the beginning of May. During the dry season, only 18–26 cm (7–10 inches) of rain fall" (Croat, 1978, p. 3). The development of a better defined and more extensive tropical dry forest in the middle Pliocene Gatun flora, compared to older Tertiary floras in the region, may mark the beginning of greater seasonality in the region as a consequence of increasing elevations and closure of the marine portal between North and South America.

"The atmospheric temperature may vary from as low as 16.5°C (61.7°F) to as high as 35.5°C (95.9°F), with the lowest temperatures being recorded within the forest during the rainy season and the highest at the Laboratory Clearing in the dry season. With rare exceptions the temperature ranges between 21° and 32°C (70° and 90°F) throughout the year, and the average ambient temperature in the Laboratory Clearing is 27°C (77°F). The seasonal variation in monthly averages is just 2.2°C. In the dry season the range of the monthly averages of diurnal temperature is 9–11°C, and during the rainy season it is 8–9°C. Thus the diurnal temperature variation is greater than the variation between seasons. Temperature on the forest floor is especially constant, the range of the average diurnal temperature being about 6.1°C" (Croat, 1978, p. 5).

The Tertiary microfossil floras known for northern Latin America have been placed on the global paleotemperature curve of Savin (1977; Savin & Douglas, 1985; Savin et al., 1975) by Graham (1987b, fig. 3). The middle Pliocene Gatun flora (previously considered late Miocene in age, Graham 1987b; middle Miocene, Stewart & Stewart, 1980) was deposited near the end of a temperature drop that began in the middle Miocene, and just before a slight rise in the late Pliocene that preceded the final fall toward glacial conditions in the Pleistocene. These temperature fluctuations, affecting vegetation in the north temperate region (Hubbard & Boulter, 1983; Tanai & Huzioka, 1967; Wolfe, 1978), also affected biotas as far south as 18°N latitude (viz., the Pliocene Paraje Solo flora of Veracruz, Mexico; Graham, 1976). However, at 9°N latitude the Tertiary floras of southern Central America (Uscari of Costa Rica; Gatuncillo, Culebra, Cucaracha, and La Boca of Panama) were deposited under a different set of physiographic conditions. To the north (eastern Mexico) the setting was continental within an area of considerable physiographic relief. To the south (the Costa Rican and Panamanian Tertiary floras) the setting was insular with less physiographic relief (Dengo, 1973; Raven & Axelrod, 1974, fig. 4). As noted by Graham (1989b, c), the existence of these two physiographic provinces within northern Latin America influenced the impact of Tertiary paleotemperature changes on the terrestrial biota. In the Paraje Solo flora of Veracruz, Mexico, the impact was augmented by communities already stressed along altitudinal gradients. The Panamanian Tertiary floras were buffered against the extremes of temperature fluctuations by communities existing under lower-altitude, insular conditions in a region of considerably less physiographic diversity. Thus, the dynamics of Tertiary paleocommunities in southern Central America were driven not so much by temperature fluctuations, as with the tropical flora of southern Mexico, or by changes in sea level (and, in consequence, water tables) as with the biota of the Amazon Basin, but by changes in physiography. These changes, first evident among presently known fossil floras in southern Central America beginning in the middle Pliocene, were relatively rapid uplift and subsidence of land surfaces, increasing altitudes producing the beginnings of a rain shadow effect, and closure of the isthmian portal which affected oceanic circulation patterns that resulted in an intensification of wet and drier seasons. The biological effects were relatively rapid changes in the number, distribution, and rate of speciation of mangrove and associated lowland vegetation elements (increasing diversity of the biota), and the development of a more complex and diverse set of communities, including, especially, the lower to middle montane and tropical dry forests.

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LEAF ARCHITECTURE OF THE CHLORANTHACEAE[1]

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Abstract

Leaves of 42 species of Chloranthaceae representing all four genera (*Sarcandra*, *Ascarina* (including *Ascarinopsis*), *Chloranthus*, and *Hedyosmum*) were cleared and examined to determine infrageneric and interfamilial relationships. Descriptions for all four genera are provided. Fifteen characters were examined, including: tooth type, secondary vein type, intramarginal vein, and leaf rank. Secondary architecture includes craspedodromous, semicraspedodromous, brochidodromous, and eucamptodromous patterns. Existing fossil evidence and proposals based on comparisons of extant genera are not sufficient to polarize these character states. The teeth in the Chloranthaceae are quite variable and three major types are characterized here. The leaf architecture of the Chloranthaceae is compared with that of the Lauraceae and Annonaceae, and, although the Chloranthaceae share a number of features in common with these two families, other characters suggest an ancient separation.

Although leaf architecture of extant angiosperms has been shown to be useful to identify fossil remains (Upchurch & Wolfe, 1987) and to elucidate intra- and interfamilial relationships (Levin, 1986a, b, c; Rury & Dickison, 1977), leaf architecture has been studied in only a relatively minute fraction of angiosperms. The leaf architecture of the Chloranthaceae is of particular interest because the position of the family in higher-order angiosperm classification is in dispute, and because some of the oldest known fossil floral parts (Friis et al., 1986) and fossil leaves (Upchurch, 1984a, b) are attributed to the Chloranthaceae. No in-depth studies have been conducted on the leaf architecture of the Chloranthaceae, and few critical studies have been conducted on leaf architecture in general. Especially few studies have been done in the Magnoliidae (Doyle & Hickey, 1976; Hickey & Wolfe, 1975; Klucking, 1986, 1987).

The Chloranthaceae are a small pantropical family with four genera and approximately 70 species. The four genera fall into two distinct groups. *Sarcandra* and *Chloranthus* are distinguished by bisexual flowers and an herbaceous or suffrutescent habit; they are confined to Indomalasia (Verdcourt, 1986). *Ascarina* and *Hedyosmum*, on the other hand, are distinguished by their unisexual flowers and arborescent or shrubby habit. *Ascarina* ranges from New Zealand to New Caledonia and Malesia with one disjunct species (originally placed in its own genus, *Ascarinopsis*) in Madagascar (Jeremie, 1980; Swamy, 1953; Verdcourt, 1985, 1986). *Hedyosmum* occurs from Mexico to Brazil and the West Indies with one disjunct species in Southeast Asia (Todzia, 1988).

Some authors have suggested that the Chloranthaceae are among the most primitive families of angiosperms and at the root of the Hamamelid and Magnoliid lines (Burger, 1977; Endress, 1987). The fossil record of the family and closely related forms dates to the Early Cretaceous and includes pollen (see Walker & Walker, 1984, for summary), leaves (Upchurch, 1984a, b), and flowers (Crane et al., 1989; Friis et al., 1986) (see Crane, 1989, for review). The Chloranthaceae also have been postulated to have an important position in the separation of the monocot and dicot phylogenetic lineages (Burger, 1977).

Furthermore, much controversy surrounds the placement of the Chloranthaceae in higher-order angiosperm classification (see Verdcourt, 1985). In recent classifications the family has been placed in the Piperales (Cronquist, 1981), Magnoliales (Dahlgren, 1980), Laurales (Takhtajan, 1980), and the Annonales (Thorne, 1976). Recent studies of floral anatomy strongly suggest placement of the

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Chloranthaceae in the Laurales near the Trimeniaceae and Amborellaceae (Endress, 1986, 1987; Endress & Sampson, 1983). Endress (1987) suggested that the family may link the Laurales and the Piperales as well as being pivotal to understanding the separation of the Hamamelidae and the Magnoliidae.

The present study was undertaken to examine the leaf architecture of the Chloranthaceae in order to provide additional information for generic circumscription and to shed new light on intrafamilial and interfamilial relationships of the family. The specific objectives of this investigation are (1) to provide a comprehensive description of the leaf architecture of the Chloranthaceae; (2) to outline basic trends of specialization in the architecture of chloranthaceous leaves; (3) to look at the relationship of leaf architecture and elevation in *Hedyosmum* species; and (4) to provide leaf architectural data that will contribute to a better understanding of the interfamilial relationships of the family.

Materials and Methods

Leaves of 45 species of Chloranthaceae representing all four genera were studied (Table 1). The most completely surveyed genus was *Hedyosmum* in which leaves of 37 of the 40 species were cleared. Leaf clearings were done following Fuchs's Method No. 1 (Fuchs, 1963) with some modification. Leaves were obtained from FAA-preserved material or dried herbarium specimens, placed in 80% ETOH for several days, and then slowly rehydrated. The specimens were subsequently placed in a solution of 1% basic fuchsin in 10% sodium hydroxide for 12–36 hours in a 60°C oven and then washed in water for several days. After dehydration, the leaves were immersed in a mixture of 3 parts absolute alcohol and 1 part concentrated HCl and then washed in absolute alcohol for 48 hours. After two xylene rinses, the specimens were mounted on slides with permount.

Leaves with thick waxy cuticles that prevented infiltration of the NaOH-basic fuchsin solution were pretreated with 100% dichloromethane. After 0.5–2.0 hours in dichloromethane, the leaves were washed in absolute alcohol before the dehydration series. Leaves with large amounts of tannin deposits that obscured the internal features were pretreated with 10% ammonium hydroxide for 1–5 minutes and then rinsed well before continuing the basic fuchsin-sodium hydroxide procedure.

Many of the principal character states and discrete features are summarized in Table 2. The only comprehensive sample here is *Hedyosmum*. One of the two species of *Sarcandra* is represented. Only small representations of *Ascarina* and *Chloranthus* are given. Five out of 20 species of *Chloranthus* and three out of 11 species of *Ascarina* were sampled.

Characters

Leaf architectural terminology generally follows Hickey (1973, 1977, 1979). Fifteen characters were examined (Table 2), the following of which require more explanation.

(8) Tooth type. The six different variants found in the Chloranthaceae were given the following codes: 1A, 1B, 2A, 2B, 2C, and 3. A detailed description of each type is provided in the discussion section.

(9) Secondary vein type. In addition to the standard brochidodromous arrangement where some secondaries are joined in a series of prominent arches, some leaves have the secondaries upturned and gradually diminishing apically inside the margin and thus are intermediate between brochidodromy and eucamptodromy. The condition where the secondary veins are not looped near the apex is designated EB, and the less common case when the unlooped secondary veins are near the base is called BE. The semicraspedodromous (S) condition may occur when secondary loops branch sending the admedial branch to join the superadjacent secondary vein and the exmedial branch to a tooth. This is seen in *Chloranthus* (Fig. 5), *Hedyosmum* (Figs. 11, 14), and *Sarcandra* (Fig. 2). A less well organized version is like the above but with some branches from secondary arches forming tertiary and higher order loops and other branches entering teeth. Upchurch (pers. comm.) calls this "festooned craspedodromous" (FC), and this can be seen in *Ascarina* (Figs. 3, 6).

(11) Presence of an intramarginal vein. This refers to a collector vein formed from the loops of the secondary veins and is usually present within 2–4 mm of the leaf margin.

(12) Presence of an intermarginal vein or fimbrial vein. This refers to the vein immediately within the leaf margin. Tertiary veins usually unite to form the fimbrial vein.

(13) Highest vein order. Leaf veins branch repeatedly, producing higher orders of venation. The primary vein (or midvein) of the leaf is the first rank with the second rank composed of secondaries or the major lateral veins. The next finer set arising from both primary and secondary veins is designated the tertiary veins and so on, until the

TABLE 1. Collection data for specimens used in Chloranthaceae leaf architecture study.

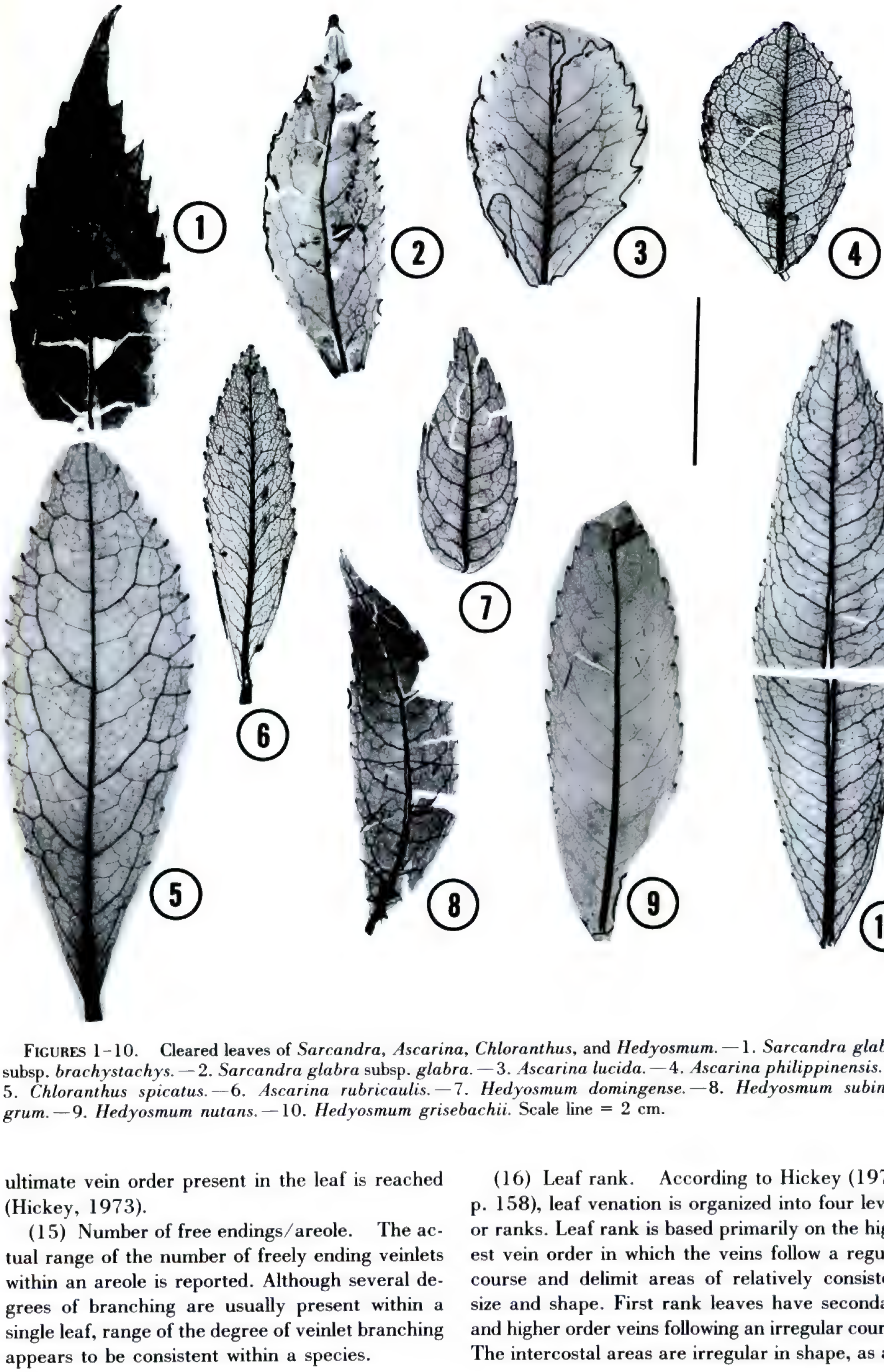
Species	Collection	Country	State or province	Elevation
Sarcandra				
S. glabra (Thunb.) Nakai subsp. *glabra*	*Wood et al. 3849* A, MO	Taiwan	Taipei Hsien	N/A
S. glabra subsp. *brachystachys* (Blume) Verdcourt	*Levine 3170* MO	China	Guangxi	N/A
Chloranthus				
C. erectus (Buch.-Ham.) Verdcourt	*J. Sinclair 6553* US	N/A	N/A	N/A
C. angustifolius Oliver	*Henry 658* GH	China	N/A	N/A
C. spicatus Pei	*C. O. Levine 693* A	N/A	N/A	N/A
Ascarina				
A. lucida Hook.f.	*Melville 6878* A	New Zealand	Westland	N/A
A. philippinensis C. B. Rob.	*Schodde 4897* US	New Guinea	N/A	N/A
A. rubricaulis Solms-Laub.	*McPherson 6486* MO	New Caledonia	Mt. Do	N/A
Hedyosmum subg. Hedyosmum sect. Orientale				
Hedyosmum orientale Merrill & Chun	*Tsang 26692* A	China	Kwangtung	N/A
Hedyosmum grisebachii Solms-Laub.	*Alain et al. 5523* GH, US	Cuba	Oriente	N/A
Hedyosmum domingense Urban	*Morton 9338* US	Cuba	Oriente	1,600–1,800 m
Hedyosmum subintegrum Urban	*Shafer 8061* NY, US	Cuba	Oriente	N/A
Hedyosmum subg. Hedyosmum sect. Hedyosmum				
Hedyosmum nutans Sw.	*Morley et al. 937* A, B, MO, S	Jamaica	Clarendon	975 m
Hedyosmum brenesii Standley	*Grayum et al. 3550* MO, TEX	Costa Rica	Limón	ca. 400 m
Hedyosmum subg. Tafalla sect. Microcarpa				
Hedyosmum pseudoandromeda Solms-Laub.	*Steyermark 91,705* F, GH, NY, US	Venezuela	Distrito Federal	2,300 m
Hedyosmum gentryi D'Arcy & Liesner	*Plowman 13,396* F, TEX	Venezuela	Fálcon	1,200–1,400 m
Hedyosmum neblinae Todzia	*Gentry & Stein 46700* MO, TEX	Venezuela	Amazonas	1,900–2,100 m
Hedyosmum arborescens Sw	*Anderson 3257* DUKE, LL, GH, US	Jamaica	Portland	1,310–1,371 m
Hedyosmum costaricense W. Burger	*Todzia 2038* CR, TEX	Costa Rica	San José	1,100 m
Hedyosmum burgerianum D'Arcy & Liesner	*Todzia & Schmalzel 2578* MO, TEX	Panama	Chiriquí	1,500–1,600 m
Hedyosmum bonplandianum HBK	*Todzia 2545* F, GH, MO, NY, TEX, US	Panama	Chiriquí	900–1,100 m
Hedyosmum racemosum (Ruiz Lopez & Pavón) G. Don	*Todzia & Grimes 2516* AAU, MO, NY, QCA, QCNE, TEX, US	Ecuador	Zamora–Chinchipe	2,500 m

TABLE 1. Continued.

Species	Collection	Country	State or province	Elevation
Hedyosmum sprucei Solms-Laub.	*Todzia & Grimes 2520* QCA, QCNE, TEX	Ecuador	Pastaza	900–1,000 m
Hedyosmum brasiliense Mart. ex Miq.	*Todzia & Hatschbach 2384* AAU, CAS, F, G, GH, F, MO, NY, S, TEX, US	Brazil	Paraná	10–25 m
Hedyosmum goudotianum Solms-Laub.	*Todzia 2391* F, GH, MO, NY, TEX, US	Colombia	Antioquia	ca. 2,500 m
Hedyosmum correanum D'Arcy & Liesner	*Todzia 2550* F, GH, MO, NY, TEX, US	Panama	Chiriquí	1,500–1,600 m
Hedyosmum colombianum Cuatrecasas	*Todzia 2425* COL, F, JAUM, MO, NY, TEX	Colombia	Cundinamarca	ca. 2,500 m
Hedyosmum crenatum Occhioni	*Todzia 2430* COL, F, HUA, JAUM, MO, NY, TEX, US	Colombia	Cundinamarca	ca. 3,100 m
Hedyosmum strigosum Todzia	*Todzia & Grimes 2530* MO, TEX, QCA, QCNE	Ecuador	Napo	2,530 m
Hedyosmum anisodorum Todzia	*Todzia & Grimes 2475* F, MO, NY, QCA, QCNE, TEX	Ecuador	Pichincha	2,000-2,500 m
Hedyosmum steinii Todzia	*Lozano 3165* COL	Colombia	Chocó	1,700–1,950 m
Hedyosmum spectabile Todzia	*Todzia & Grimes 2515* MO, NY, QCA, QCNE, TEX	Ecuador	Zamora–Chinchipe	2,500 m
Hedyosmum scaberrimum Standley	*Todzia 2539* MO, TEX	Panama	Coclé	780–900 m
Hedyosmum translucidum Cuatrecasas	*Todzia 2417* AAU, COL, JAUM, MO, NY, PSO, TEX	Colombia	Putumayo	2,600–2,800 m
Hedyosmum dombeyanum Solms-Laub.	*Todzia & Stein 2699* F, GH, NY, MO, TEX, US, USM	Peru	San Martín	1,900–1,950 m
Hedyosmum lechleri Solms-Laub.	*Todzia & Stein 2733* F, MO, TEX, USM	Peru	Huánuco	2,400 m

TABLE 1. Continued.

Species	Collection	Country	State or province	Elevation
Hedyosmum subg. Tafalla sect. Artocarpoides				
Hedyosmum mexicanum Cordemoy	*Todzia & Schmalzel 2580* MO, TEX	Panama	Chiriquí	1,800 m
Hedyosmum subg. Tafalla sect. Macrocarpa				
Hedyosmum scabrum (Ruiz Lopez & Pavón) Solms-Laub	*Todzia & Grimes 2514* F, MO, NY, QCA, QCNE	Ecuador	Loja	2,700 m
Hedyosmum angustifolium (Ruiz Lopez & Pavón) Solms-Laub	*Todzia & Stein 2764* TEX, USM	Peru	Junín	1,300–1,400 m
Hedyosmum maximum (Kuntze) K. Schumann	Steinbach 591 GH, MO, NY, US	Bolivia	Cochabamba	3,450 m
Hedyosmum cumbalense Karsten	*Todzia & Grimes 2492* MO, QCA, TEX	Ecuador	Carchi	3,200–3,300 m
Hedyosmum parvifolium Solms-Laub.	Luteyn 5331 AAU, COL, MO, NY, US	Venezuela	Táchira	2,500–3,200 m
Hedyosmum cuatrecazanum Occhioni	*Todzia & Grimes 2505* F, MO, NY, QCA, QCNE, TEX, US	Ecuador	Azuay	2,600–2,800 m
Hedyosmum luteynii Todzia	*Todzia & Grimes 2480* MO, NY, QCA, QCNE, TEX, US	Ecuador	Napo	3,000–3,100 m
Hedyosmum peruvianum Todzia	*Todzia & Stein 2731* AAU, F, GH, K, MO, NY, TEX, USM	Peru	Huánuco	2,400–2,600 m



FIGURES 1–10. Cleared leaves of *Sarcandra, Ascarina, Chloranthus,* and *Hedyosmum.*—1. *Sarcandra glabra* subsp. *brachystachys.*—2. *Sarcandra glabra* subsp. *glabra.*—3. *Ascarina lucida.*—4. *Ascarina philippinensis.*—5. *Chloranthus spicatus.*—6. *Ascarina rubricaulis.*—7. *Hedyosmum domingense.*—8. *Hedyosmum subintegrum.*—9. *Hedyosmum nutans.*—10. *Hedyosmum grisebachii.* Scale line = 2 cm.

ultimate vein order present in the leaf is reached (Hickey, 1973).

(15) Number of free endings/areole. The actual range of the number of freely ending veinlets within an areole is reported. Although several degrees of branching are usually present within a single leaf, range of the degree of veinlet branching appears to be consistent within a species.

(16) Leaf rank. According to Hickey (1977, p. 158), leaf venation is organized into four levels or ranks. Leaf rank is based primarily on the highest vein order in which the veins follow a regular course and delimit areas of relatively consistent size and shape. First rank leaves have secondary and higher order veins following an irregular course. The intercostal areas are irregular in shape, as are

TABLE 2. Leaf architecture data. (1) In *Hedyosmum* the sectional alignments are given as follows: * subg. *Hedyosmum* sect. *Orientale*; ◇ subg. *Hedyosmum* sect. *Hedyosmum*; + subg. *Tafalla* sect. *Microcarpa*; ! subg. *Tafalla* sect. *Microcarpa*; ● subg. *Tafalla* sect. *Macrocarpa*. (2) & (3) Data representative for species, not just individual cleared leaves. (4) Leaf shape: el = elliptic, la = lanceolate, li = linear, n = narrowly, ob = obovate, ov = ovate, w = widely. (5) Average leaf length/width ratio. (6) Leaf apex: acm = acuminate, act = acute, b = broadly, l = long, ob = obtuse. (7) Leaf base: cun = cuneate, n = narrowly, obt = obtuse, rd = rounded, trun = truncate. (8) Tooth type: see text for discussion. (9) Secondary vein type: B = brochidodromous, S = semicraspedodromous, E = eucamptodromous, FC = festooned craspedodromous. (10) Average number of major secondary veins per leaf side. (11) Presence or absence of an intramarginal vein. (12) Presence or absence of an intermarginal (or fimbrial) vein. (13) Highest vein order. (14) Areole size. 1 = very large >2 mm, 2 = large 2–1 mm, 3 = medium 1–0.3 mm, 4 = small <0.3 mm. (15) Number of free vein endings/areole. (16) Leaf rank explained in text.

(1) Species	(2) Length (cm)	(3) Width (cm)	(4) (Shape)	(5) l/w ratio	(6) Apex
S. glabra subsp. *glabra*	2–20	1–8	la to el	2.4:1	l-acm
S. glabra subsp. *brachystachys*	2–20	1–8	la to el		l-acm
C. erectus	8–29*	3–13*	el	5:1	acm
A. lucida	2–7	2–4	el, ov	1.5:1	act
A. philippinensis	3–14(–18)	2–8(–10)	el, ob, ov	1.7:1	ob, acm
A. rubricaulis	5–12	1–3	la	4.2:1	acm
**H. orientale*	(9–)15–25	1–3	la to li-ob	10:1	l-acm
**H. grisebachii*	7–13	2–3	la to ob-la	4:1	l-acm
**H. domingense*	4–6(–8)	1–2	la to n el	3.3:1	acm
**H. subintegrum*	(2–)5–8	1–2	n el, n ob	4.3:1	acm
◇*H. nutans*	5–14	1–2	la	6.3:1	acm
◇*H. brenesii*	6–16	1–4	li-la, n el	4.4:1	l-acm
+*H. pseudoandromeda*	3–4(–6)	2–3	el, n el	1.4:1	act
+*H. gentryi*	6–16	3–6	ob to el	2.4:1	acm
+*H. neblinae*	(4–)6–9	3–6	ov to w el	1.7:1	act, acm
+*H. arborescens*	(3–)5–12(–18)	2–6	el	2.1:1	l-acm
+*H. costaricense*	(4–)8–15(–20)	2–5(–7)	n el, el	3.3:1	l-acm
+*H. burgerianum*	3–6	1–2	ov to ob	3:1	l-acm
+*H. bonplandianum*	5–13(–17)	(2–)4–7	n el, el, ov	1.6:1	acm
+*H. racemosum*	6–23	3–8	ob, el, ov	2.6:1	acm
+*H. sprucei*	(5–)8–19(–22)	(2–)4–8	n el, n ob	2.2:1	acm
+*H. brasiliense*	8–21	2–6(7)	n ov, n ob	3.6:1	acm
+*H. goudotianum*	(3–)6–16(–19)	2–7(–8)	n el, ov, ob	2.4:1	acm
+*H. correanum*	(3–)5–9	1–4	ov, ob, el	2.8:1	acm
+*H. colombianum*	6–15(–18)	2–7	el, ob	2.5:1	acm
+*H. crenatum*	(4–)5–11(–14)	2–4(–5)	n el, el	3:1	acm
+*H. strigosum*	8–17(–21)	3–8	el to n el	2.1:1	acm
+*H. anisodorum*	(9–)14–22(–29)	5–8(–10)	n el, n ob	2.8:1	acm
+*H. steinii*	4–12	2–5	n el, el	2.3:1	acm
+*H. spectabile*	(6–)10–20	(3–)5–8	el, ov	2.3:1	acm
+*H. scaberrimum*	(5)8–27	3–6(–8)	el, n el	3.9:1	acm
+*H. translucidum*	5–12(–16)	2–4(–5)	n ob, n el	2.4:1	acm
+*H. dombeyanum*	5–10	2–5	n el, ob	2.1:1	acm
+*H. lechleri*	4–12	2–4	n el, el	2.7:1	acm
!*H. mexicanum*	10–25	2–7	la, ob-la	3.9:1	l-acm
●*H. scabrum*	6–13(–16)	2–7	n el, el, ob	2.1:1	acm
●*H. angustifolium*	(5–)12–17	2–5	la, el, ob-la	4.1:1	acm
●*H. maximum*	8–14	4–6	el	2.2:1	acm
●*H. cumbalense*	1–5	0.5–2	n el, el, ob	2.4:1	acm
●*H. parvifolium*	(2–)4–9	2–3	n el, el, ob	2.6:1	act, acm
●*H. cuatrecazanum*	(5–)8–19	2–8	ob, n ob, n el	2.7:1	acm
●*H. luteynii*	4–8(–13)	3–5(–8)	ob, el	1.5:1	acm
●*H. peruvianum*	(8-)12–22	(3–)5–9	n el, el	2.4:1	acm

TABLE 2. Continued.

(7) Base	(8) Tooth type	(9) 2° vein type	(10) 2° vein no.	(11) Intra mar. vein	(12) Inter mar. vein	(13) Highest vein	(14) Areole size	(15) No. vein end-ings	(16) Leaf rank
cun	2B	S	4–5	−	+	5	2	1–5	$2r^0$
cun	2B, 2C	EB	8	−	−	5	2	0–2	$1r^1$
cun	2B	EB, S	6–9	−	−	6	3	0–2	—
cun	3	FC	7	−	−	4–5	2	0–5	$2r^0$
cun	2A	EB	9	−	±	5	2–3	0–2	$2r^1$
cun	2A	FC	10	−	−	5	2–3	0–4	$2r^1$
n cun	2B	EB	18	−	−	4–5	2	0–1	$2r^0$
cun	1, 2A	EB	16	+	+	5	2	0–3	$2r^1$
rd	2A	B	7	−	+	5	2	2–4	$2r^3$
cun	1	BE	8	−	+	5	3	2–3	$2r^1$
rd, cun	1, 2A	S	10	−	+	5	2	0–3	$2r^2$
cun	2B	E	15	−	+	5	2–3	0–2	$2r^1$
obt, cun	2A	B	14	+	+	5	3	0–2	$2r^2$
b cun	2A	EB	12	+	+	5	2	1–3	$2r^3$
obt, trun	2A	EB	11	+	+	5	1	0–2	$2r^3$
cun, obt cun	2B	EB, S	13	+	+	5	2	0–2	$3r^0$
rd, b cun	2A	E	9	+	+	5	2	0–2	$2r^2$
cun	2A, 2B	EB	8	±	±	5	2	0–2	$2r^2$
cun, obt cun	2B	E	8	−	−	5	2	0–3	$2r^1$
cun, obt cun	1B	E	5–12	−	±	5	2	0–3	$3r^1$
cun, obt cun	1	E	11	−	−	5	3	0–3	$3r^1$
cun, obt cun	1B, 2A	EB	8	−	−	5	2	0–3	$2r^0$
cun, obt cun	3	E or B	8	−	−	5	2	2–3	$4r^0$
cun	3	E	7	−	−	5	2	0–2	$2r^1$
cun	2A	E	11	−	−	5	2–3	0–2	$2r^1$
cun, obt cun	1B, 2A	E	6	−	−	5	2	0–2	$3r^0$
rd, obt rd	1A	E	N/A	−	−	5	2	0–2	$3r^0$
n cun	3	E	9	−	±	5	2	0–2	$2r^1$
cun, obt cun	3	E	7	+	−	5	2	0–2	$2r^1$
cun, rd	3	E	6	−	−	5–7	2	0–6	$4r^0$
cun, obt cun	3	E	6–12	−	−	5	2	0–2	$2r^1$
cun, obt cun	3	E	10–12	−	−	5	2	0–3	$2r^3$
cun	2A	E	8–10	+	−	5	2	0–2	$2r^1$
obt, cun	1B	EB	9	+	−	5	2	0–2	$2r^1$
cun, obt cun	1A, 1B, 2A	E	12–14	−	−	5	2	0–3	$2r^3$
cun	1A	B	20	±	±	5	2	0–1	$3r^3$
cun, obt cun	1B	EB	15	−	−	5	2	0–2	$2r^3$
b cun, obt cun	1A	EB	10	−	−	5–6	2–3	0–4	$2r^2$
rd, trun	1B	EB	13	±	±	5	2	0–2	$2r^3$
cun, obt	2A	E	16	−	−	5	2	0–2	$2r^3$
cun, ob cun	1B	EB	14	−	±	5	2–3	0–2	$3r^0$
n-b-obt cun	1A	B	16	−	±	5	2	0–2	$3r^0$
cun, obt cun	1B	E	18	−	±	5	3	0–2	$3r^1$

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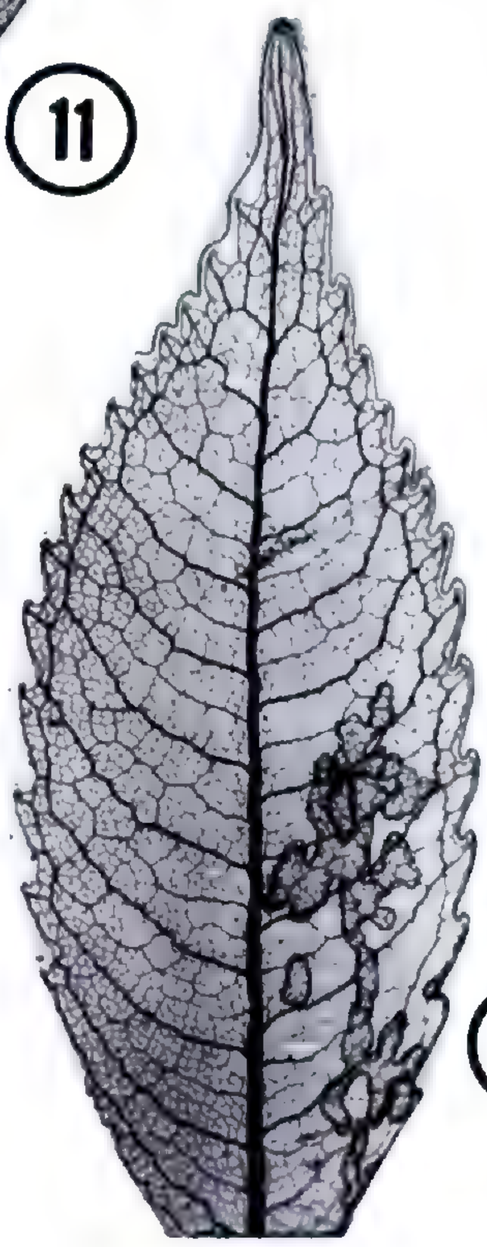

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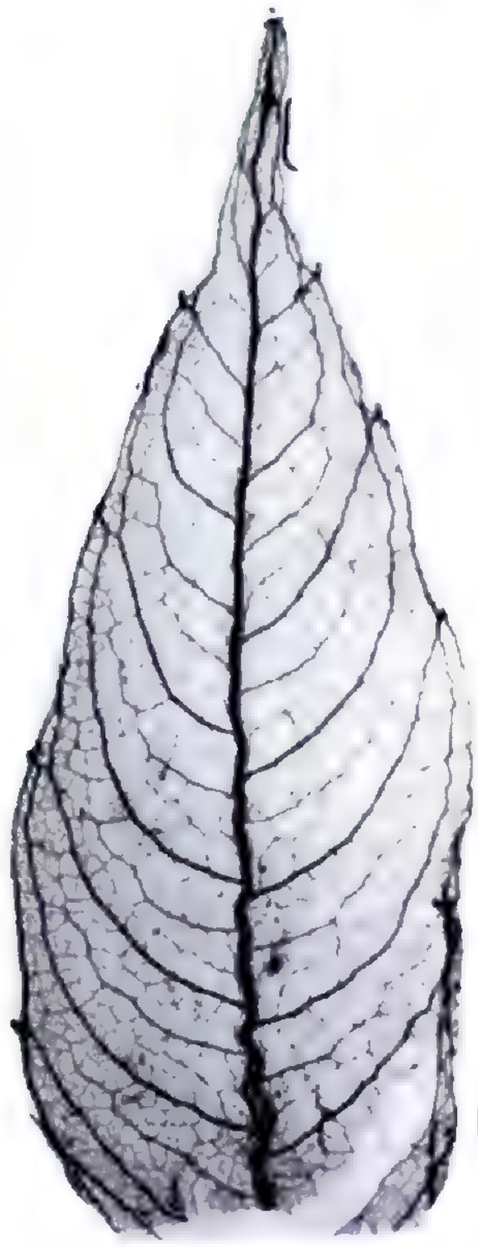

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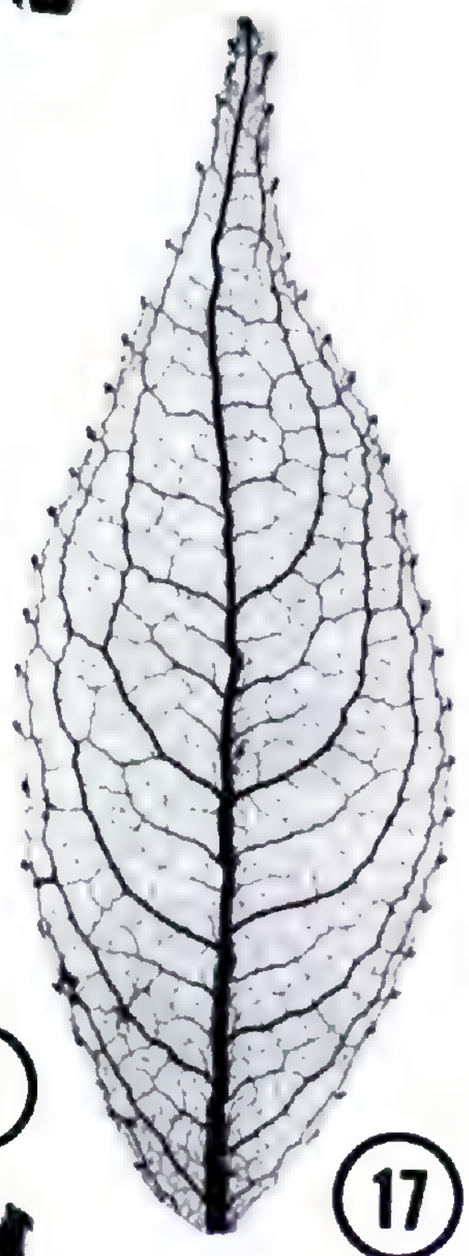

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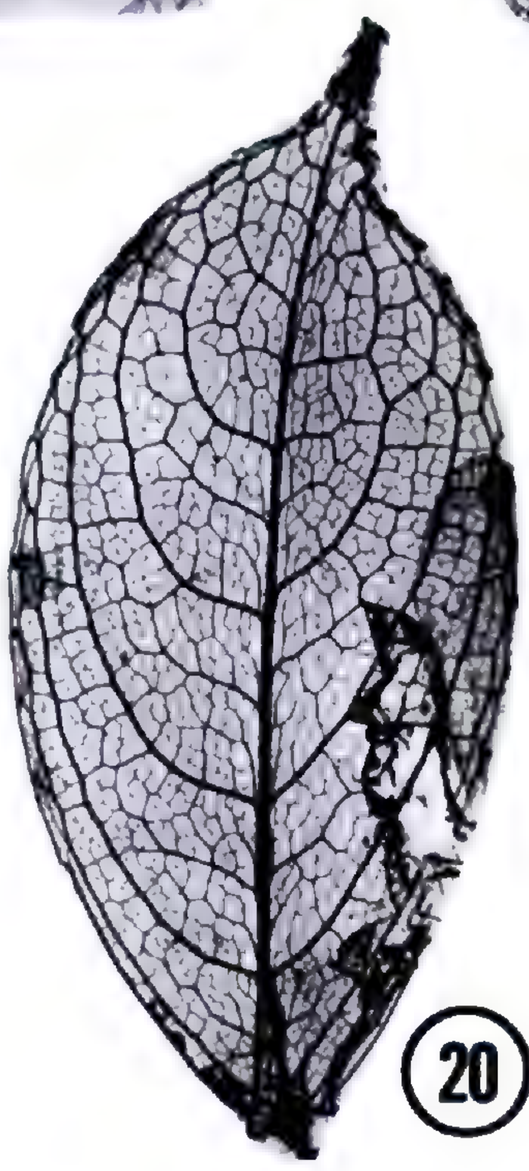

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the tertiary and quaternary domains. Domains are areas delimited by veins of tertiary and higher rank. Second rank leaves have regularly shaped intercostal areas, but higher domains are not uniform in size or shape. Third rank leaves have relatively consistent (predictable) tertiary domains. Fourth rank leaves have areoles of predictable or uniform size and shape.

Within each of the main ranks, subranks 0–3 are recognized based on the degree of advancement (increasing regularity of pattern) toward the next level. The assignment of subranks would be based on the assessment of the status of the following kinds of morphoclines. Secondary and higher order veins may arise from the next lower level at decurrent, acute, orthogonal, or obtuse angles. Vein endings within areoles may be a high number, a low number, rare, or absent. In a brochidodromous leaf there may be several orders of loops, few loops (festooned), no loops, and finally, the straightening of the arches into an intramarginal vein. In each of these sequences, one would assign a low subrank (0–1) for the beginning of the morphocline and high subrank (2–3) at the other end of the morphocline. These sequences are read in a direction of increasing specialization as supported by analyses of fossil floras. Leaves with low rank appear first in the fossil record, and it seems that leaf venation rank order correlates with the degree of advancement of the whole plant as determined by other evidence (Doyle & Hickey, 1976; Hickey, 1977; Hickey & Wolfe, 1975; Thomas & Spicer, 1987).

Leaf length and width were plotted in scatter diagrams using log scales. Samples of up to ten specimens were used for each species, if available.

Generic Descriptions

Sarcandra Gardner (figs. 1, 2, 45, 46)

Leaves elliptic, chartaceous, with length/width ratios of 3–4:1. The apex acuminate and the base cuneate to decurrent. Margin usually boldly toothed with deeper sinuses than the other genera. Sinuses rounded. The median vein to the tooth apex arising from secondaries. Petiole very short with a decurrent wing of laminar tissue on petiole. Secondary venation either semicraspedodromous or brochidodromous with basal secondary veins forming loops but tending toward eucamptodromy. Secondary veins alternate, widely spaced with about five per side, arising at an acute angle and curving apically. Intercostal areas large and irregular. Intersecondaries, about two per intercostal area, mostly simple but sometimes composite. Tertiary veins acute admedially and exmedially. Tertiary and quaternary domains both random polygonal. Highest vein resolution five. Areole development imperfect, arrangement random, and irregularly shaped. Areoles 1–2 mm with 0–5 veinlets per areole. Druses random or absent. Stone cells present in loose clusters near the midvein.

Chloranthus Sw. (fig. 5)

Leaves 4–30 cm long, elliptic, with length/width ratios of 3–5:1. The apex acuminate and the base cuneate to decurrent. Margin serrate with teeth closely adjacent to the shallow, rounded sinus. Basal side of tooth slightly convex. The tooth hydathodal with one or more large stomates on the tooth surface distal to the dilated median vein of the tooth. Leaf texture chartaceous and the petiole very short with a decurrent wing of laminar tissue. Secondary venation brochidodromous with a broad row of marginal loops or distally brochidodromous and proximally eucamptodromous with marginal loops that produce tooth veins. Secondary veins acute, usually widely spaced, with 6–9 per side of the midvein, alternate or subopposite. Intercostal areas irregular and gradually apically curving. Intersecondaries common, 1–2 per intercostal area, and ranging from simple or composite. Tertiary and quaternary domains irregularly polygonal in size and shape. Highest vein resolution five. The imperfectly developed areoles polygonal and randomly arranged, and about 0.5–2.5 mm long. Stomates common and randomly arranged over the abaxial epidermis. Prismatic crystals occurring singly or in clusters and randomly distributed in the lamina, often in and near teeth but also closer to the midvein. The clusters not like druses but appearing eroded.

Ascarina J. R. & G. Forst. (figs. 3, 4, 6)

Leaves elliptic, with length/width ratios of 1.5–4.2:1. The apex acuminate to obtuse and the base cuneate. Margins serrate with the tooth apex close

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Figures 11–20. Leaf clearings of Hedyosmum.—11. *H. gentryi.*—12. *H. pseudoandromeda.*—13. *H. neblinae.*—14. *H. burgerianum.*—15. *H. arborescens.*—16. *H. costaricense.*—17. *H. racemosum.*—18. *H. brasiliense.*—19. *H. mexicanum.*—20. *H. bonplandianum.* Scale line = 2 cm.

to the sinus. The sinus rounded. Leaf texture chartaceous to coriaceous. Petiole very short, with a decurrent wing of laminar tissue. Secondary venation a combination of festooned brochidodromous and semicraspedodromous, the secondary veins forming a series of loops near the margin and branches of looping secondary veins enter the teeth. *Ascarina philippinensis* with regular brochidodromous arches. *Ascarina rubricaulis* with strongly decurrent intersecondary veins arising either from the midvein or from a secondary vein. Other *Ascarina* species with ± nondecurrent intersecondary veins that arise only from the midvein, as in *Sarcandra* and *Chloranthus*. The 6–8 secondary veins producing somewhat regular to very regular intercostal areas. A few simple or composite intersecondary veins present. Tertiary and quaternary veins forming irregular and polygonal domains. Highest vein order 4–5. The randomly arranged areoles imperfect and irregular to polygonal. Areoles 0.3–1 mm and showing strong tendency to be elongate and parallel to the secondary veins or at right angle to the midvein. Crystals absent. Stone cells free or clustered near the midvein, or in short rows along the midvein.

Hedyosmum sw. (figs. 7–44, 47, 48, 49)

Leaves ovate to oblanceolate, elliptic, obovate varying in size from 1 to 29 cm, with length/width ratios of 1.5–10:1. The apex mostly acuminate to occasionally obtuse and the base mostly cuneate to truncate or obtuse. Margin serrate with various forms of glandular teeth. Most teeth convex basally with a small, rounded sinus. The tooth apex often close to the sinus. Texture chartaceous to coriaceous. The petiole very short with a decurrent wing of laminar tissue. Secondary venation brochidodromous, eucamptodromous, or transitional, and occasionally looped. Venation occasionally semicraspedodromous. Brochidodromous arches occasionally aligned forming an intramarginal vein. Secondaries often more numerous than 12–15 per side, acute and curving apically. Intercostal areas often very regular. Intersecondaries absent or present as simple or composite. Tertiary and quaternary veins usually irregular and polygonal. Highest vein order present usually 5 (rarely to 7). Areole development imperfect to well developed in about 20% of the species. Areole shape polygonal to irregular, usually randomly oriented. Size quite variable within a specimen and varies for the genus between 0.3 and 2.0 mm. Veinlets varying from 0–1 to 2–4 or 0–6 per areole and sometimes branched several times. Crystals absent. Sclerenchyma varied, stone cells, single or clustered, branched spongy mesophyll cells and branched vein sheath cells.

Discussion

Interpretation of character state polarities begins with the analyses of Hickey & Wolfe (1975), Doyle & Hickey (1976), and Doyle (1978). Hickey and Wolfe derive most of their conclusions from comparisons of leaf clearings based on the approximately 20,000 specimens represented in the two major cleared leaf collections in the United States. Doyle's (1978) and Hickey & Doyle's (1977) reviews comment on the one stratigraphic sample that has been analyzed in detail for both pollen and leaf fossils, the Potomac formation of the eastern United States. From those works, it appears that the earliest known angiosperm leaves are simple, entire, pinnately veined, first rank forms, with several orders of anastomosing veins and freely ending veinlets. The earliest forms illustrated in those studies show a festooned brochidodromous secondary architecture of Hickey's (1979) system. Hickey & Taylor (1989) have refined this model using cladistic comparisons of primitive genera with suggested angiosperm sister groups and with Early Cretaceous angiosperm fossils. The "ancestral angiosperm leaf" is conjectured to have a sheathing base with 4–5 separate vascular bundles entering the petiole producing pinnate (brochidodromous) or palmate (palinactindromous) venation in ovate leaves. Chloranthoid teeth are found near the apex.

In the chloranthaceous leaves conforming most

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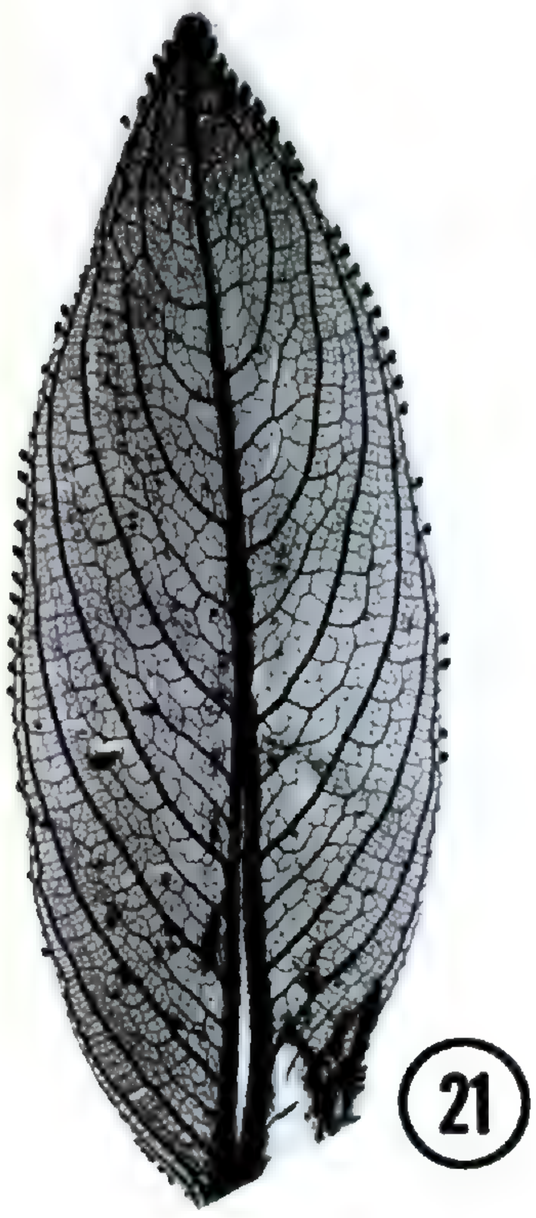
Figures 21–28. Leaf clearings of *Hedyosmum*.—21. *H. goudotianum*.—22. *H. colombianum*.—23. *H. correanum*.—24. *H. crenatum*.—25. *H. steinii*.—26. *H. spectabile*.—27. *H. anisodorum*.—28. *H. strigosum*. Scale line = 2 cm.

Figures 29–33. Leaf clearings of *Hedyosmum*.—29. *H. scaberrimum*.—30. *H. dombeyanum*.—31. *H. translucidum*.—32. *H. lechleri*.—33. *H. sprucei*. Scale line = 2 cm.

Figures 34–40. Leaf clearings of *Hedyosmum*.—34. *H. scabrum*.—35. *H. parvifolium*.—36. *H. cumbalense*.—37. *H. angustifolium*.—38. *H. cuatrecazanum*.—39. *H. peruvianum*.—40. *H. luteynii*. Scale line = 2 cm.



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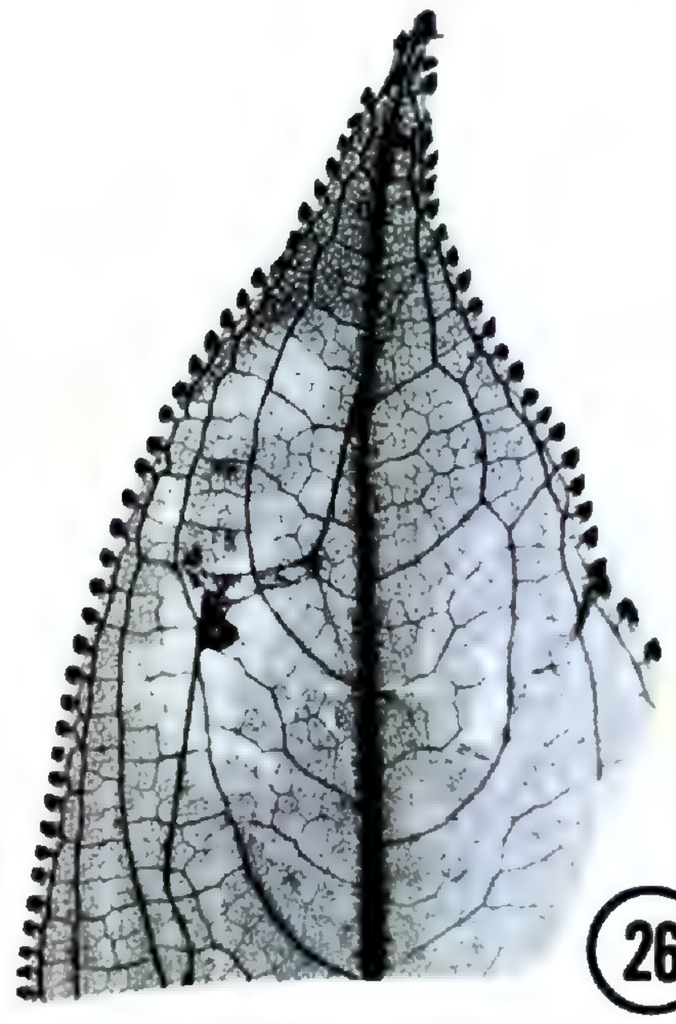

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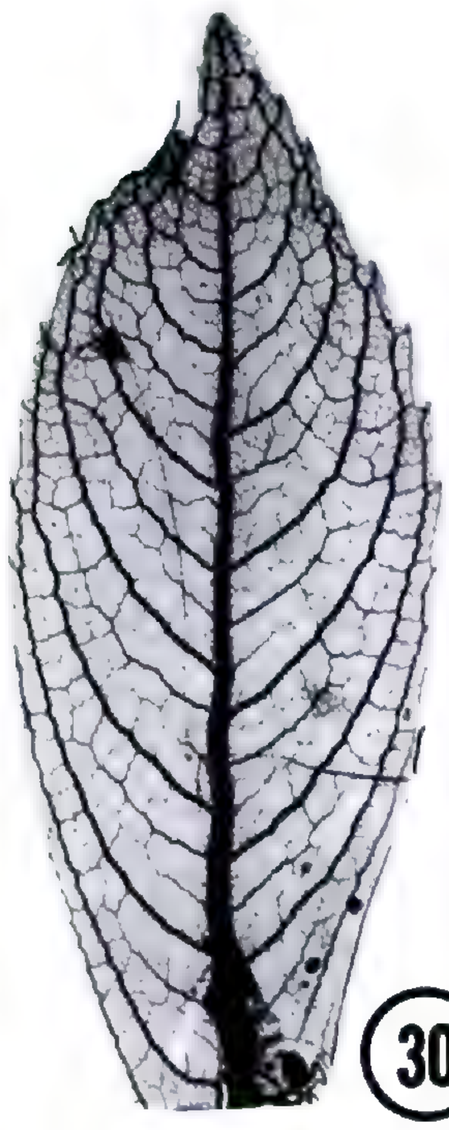

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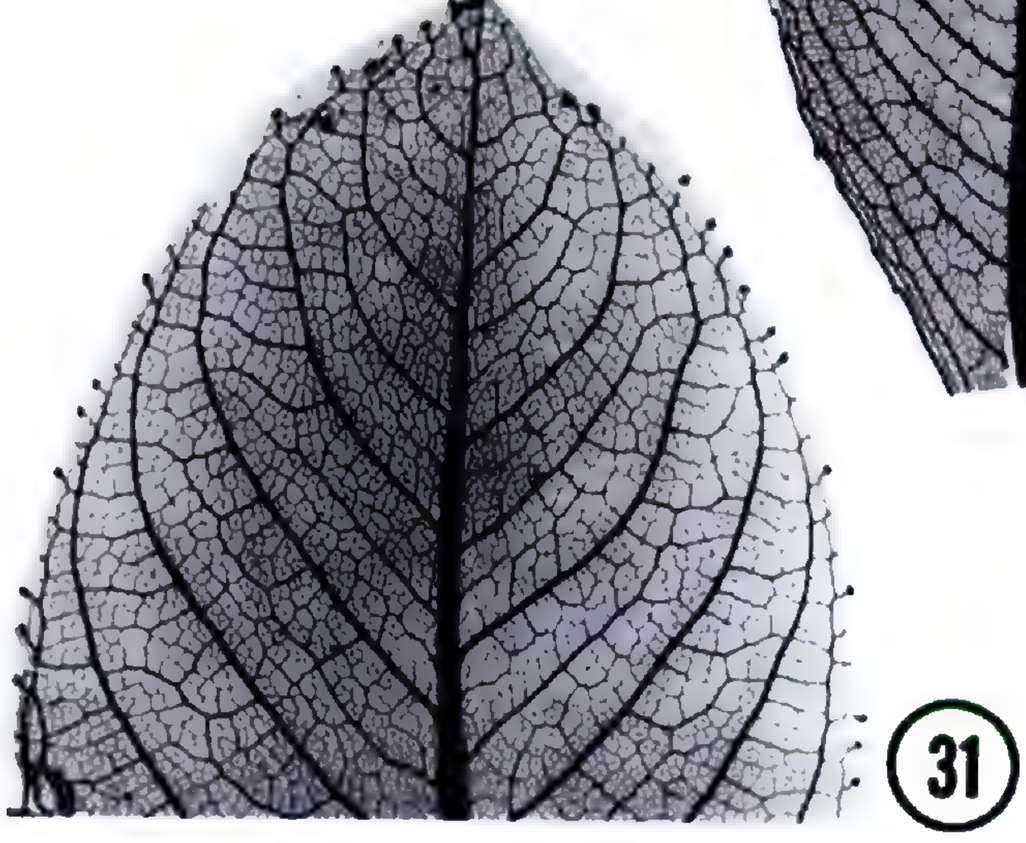

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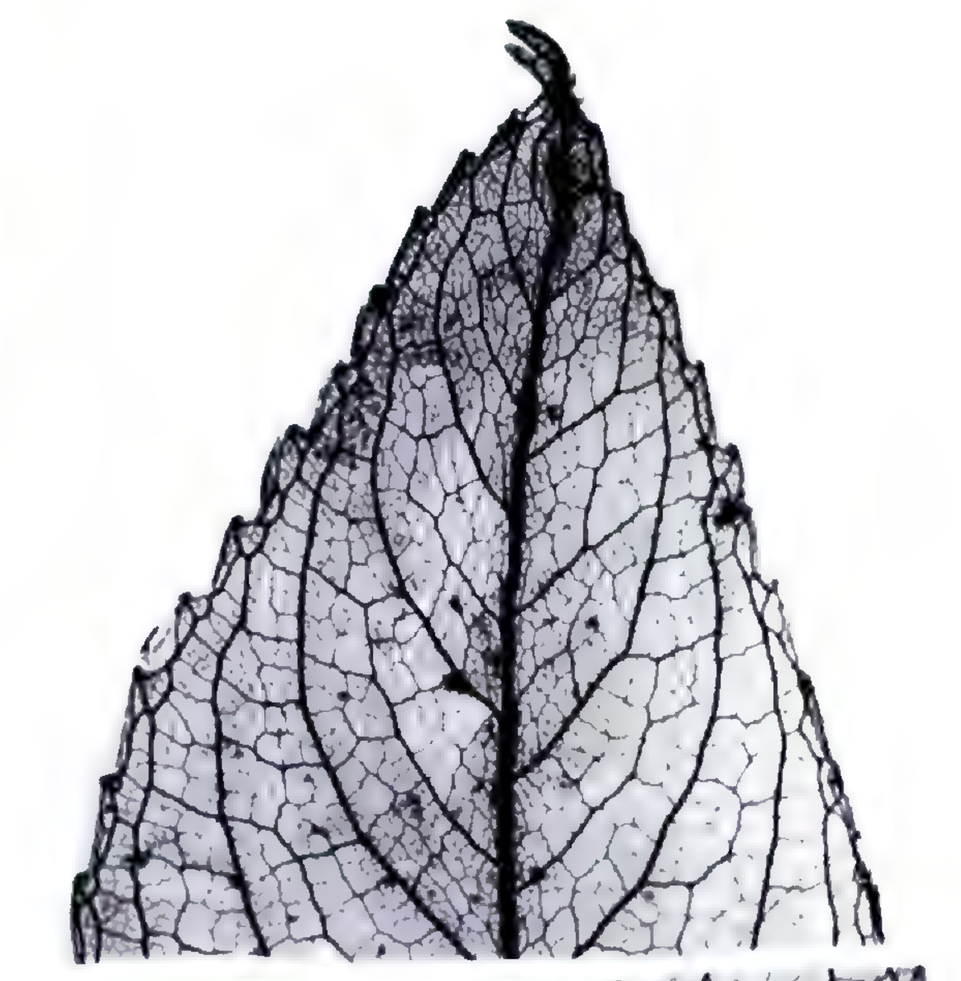

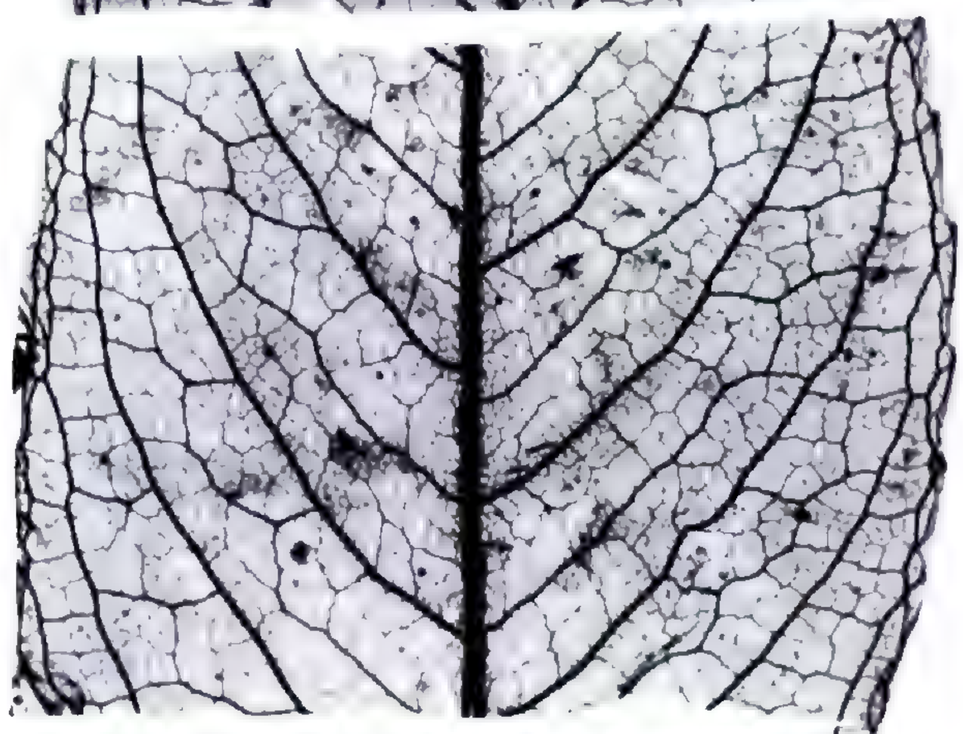

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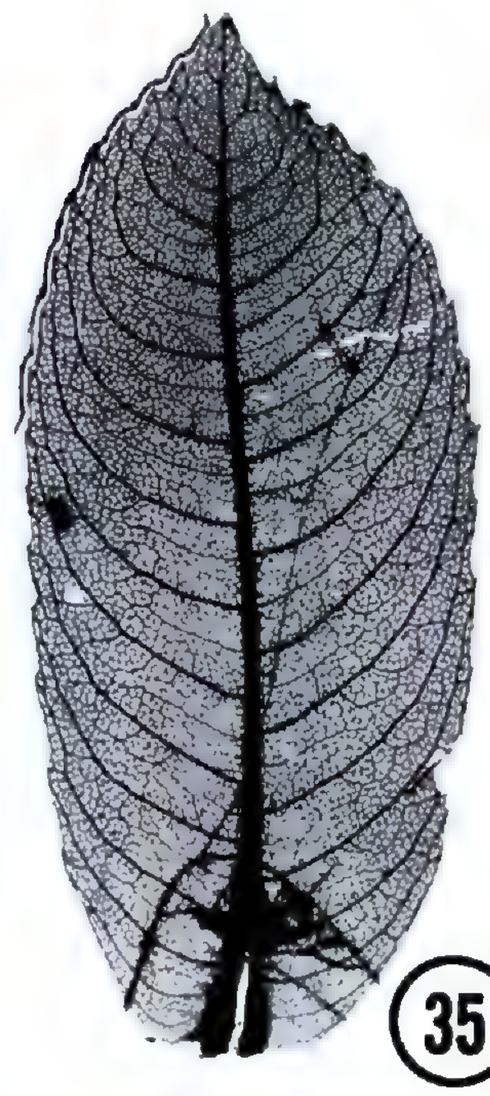
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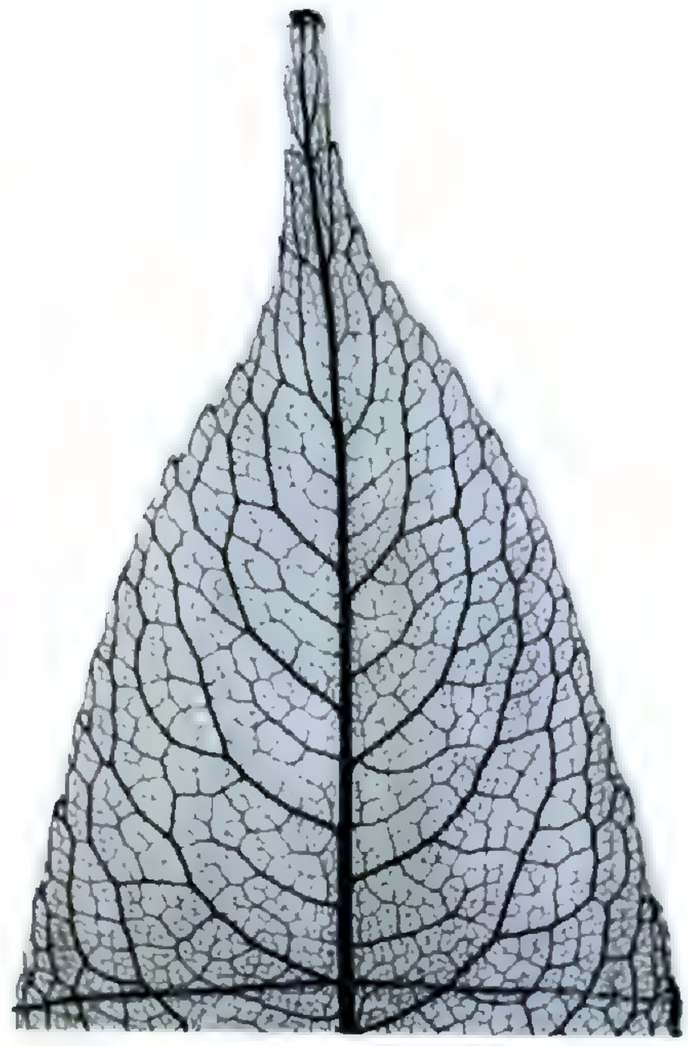
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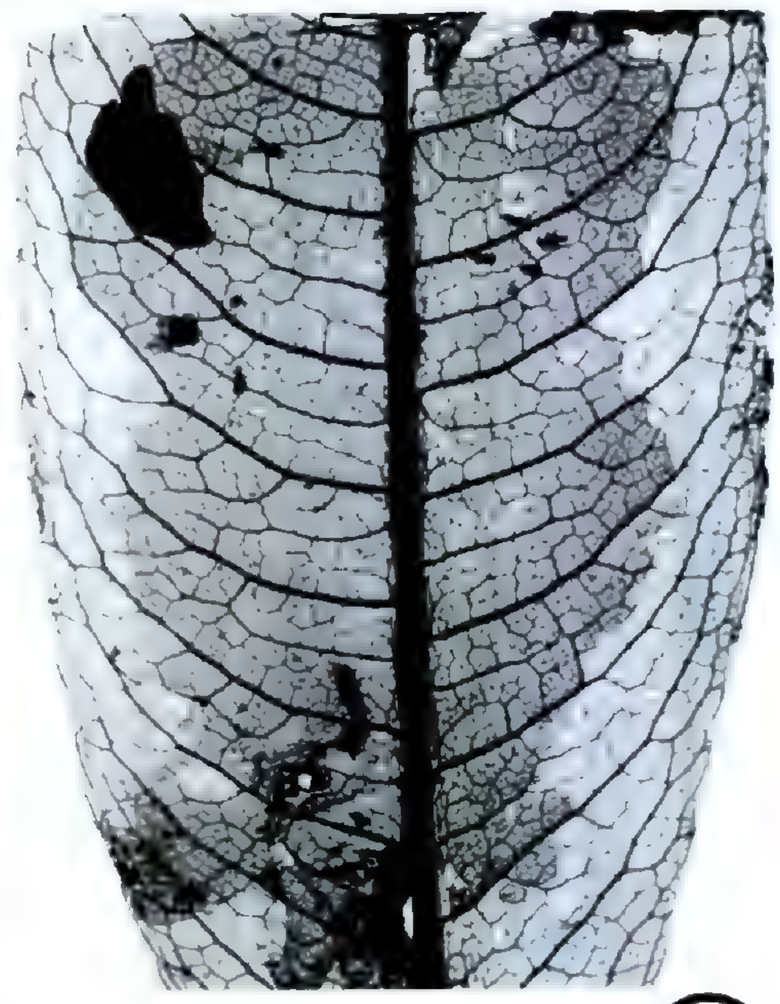
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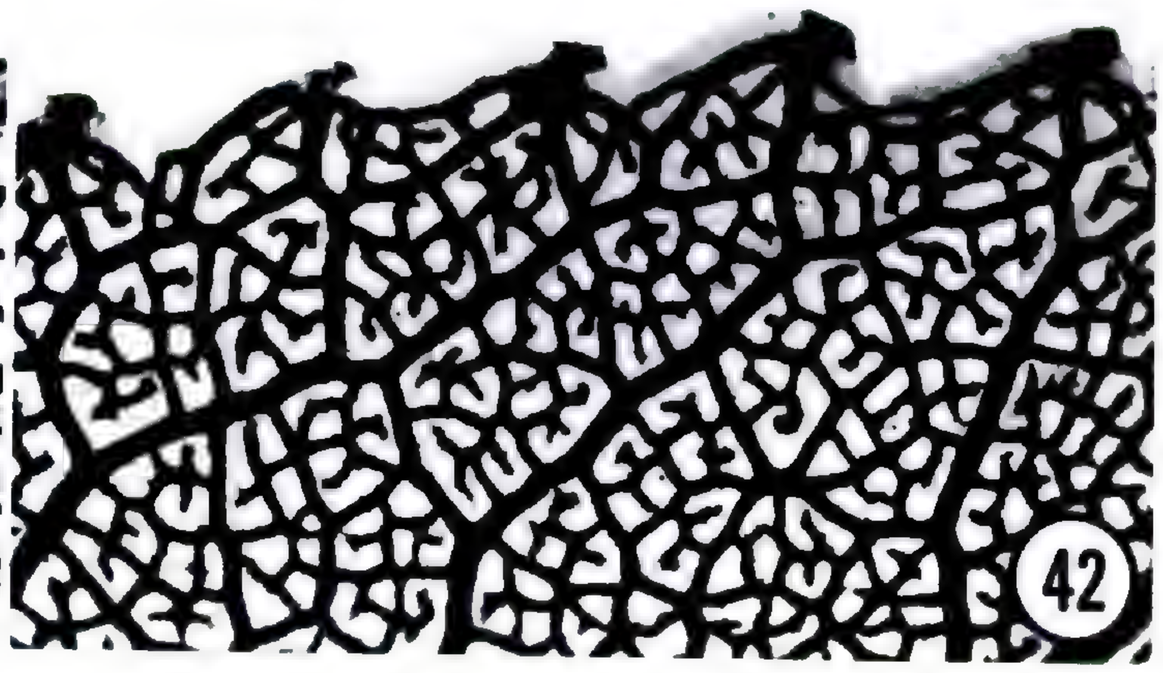
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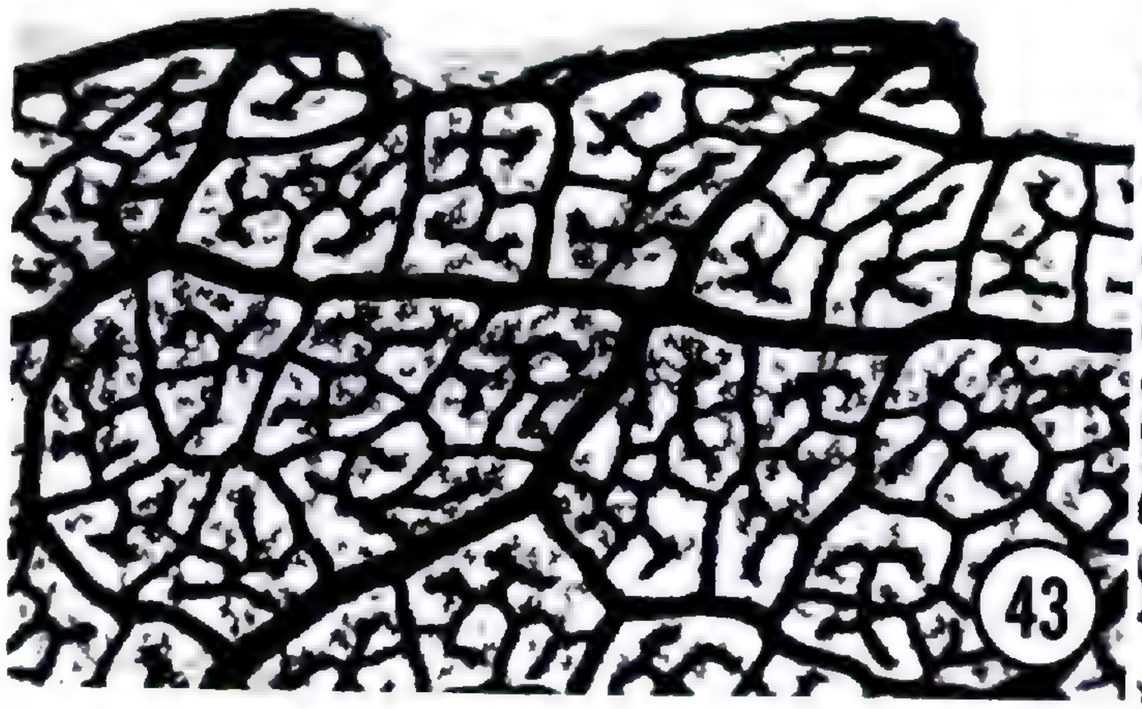
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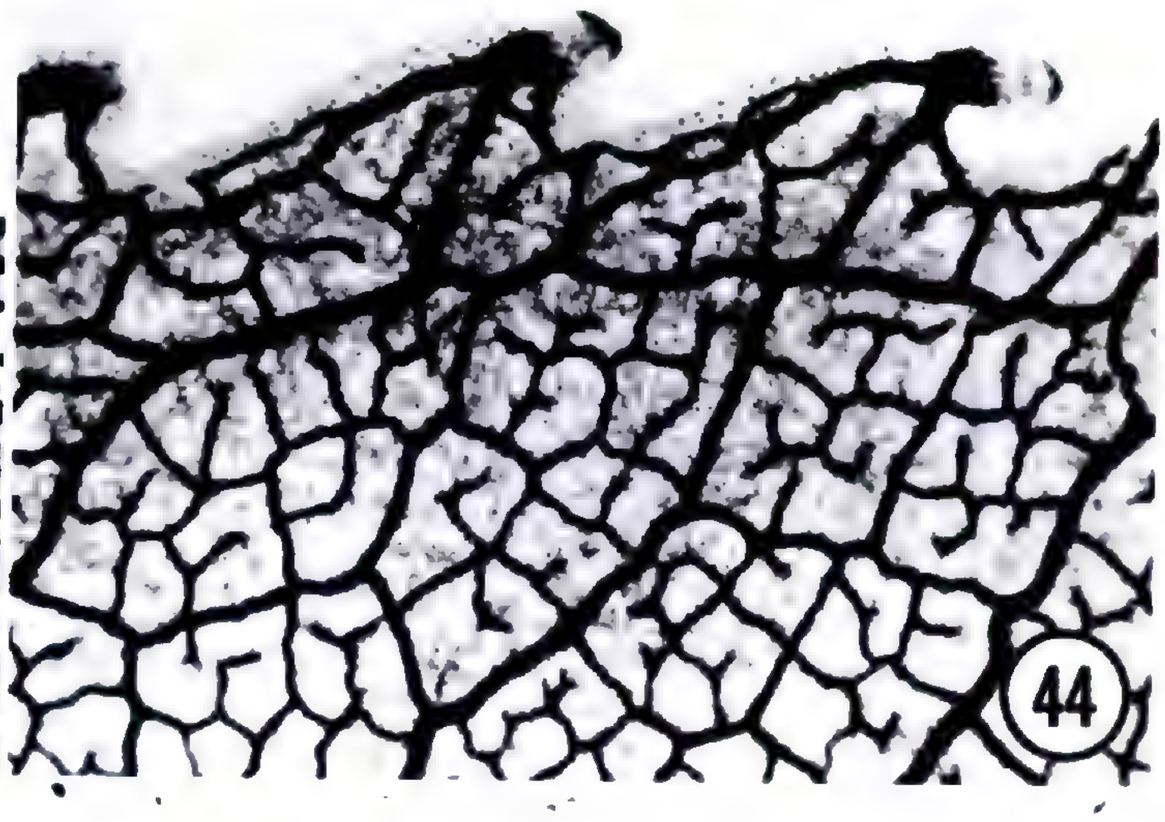
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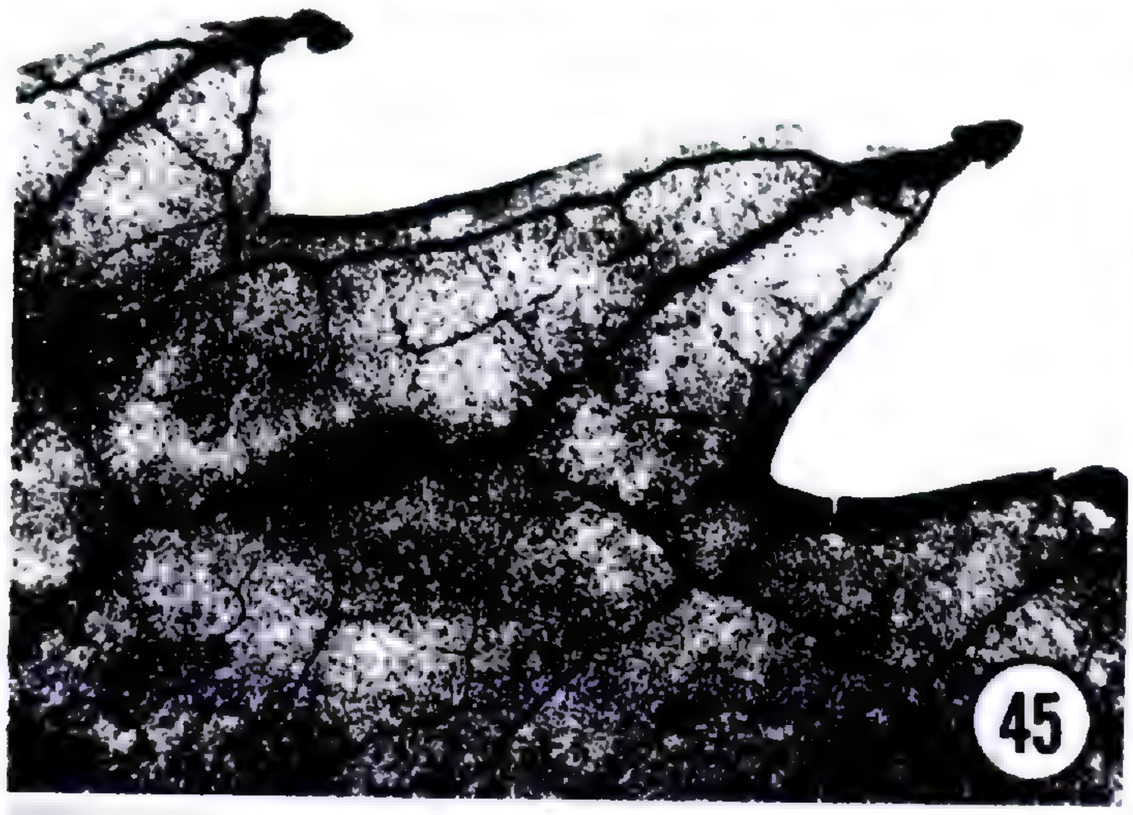
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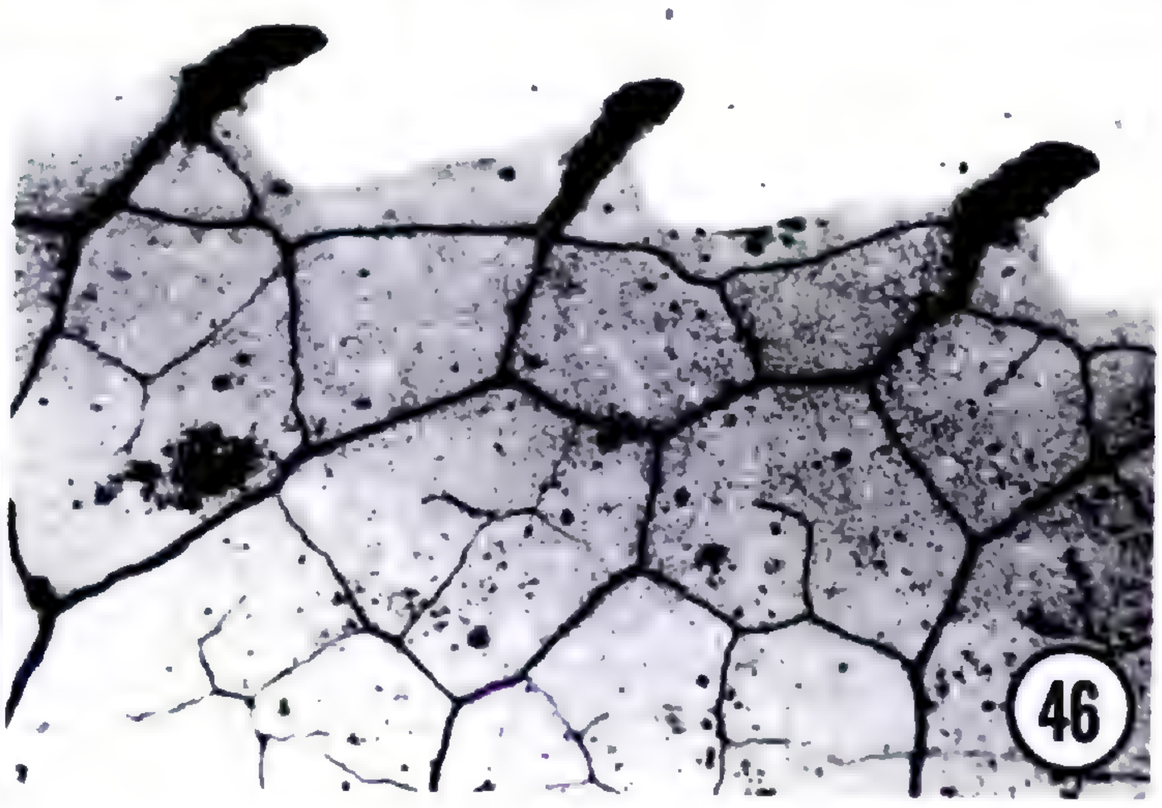
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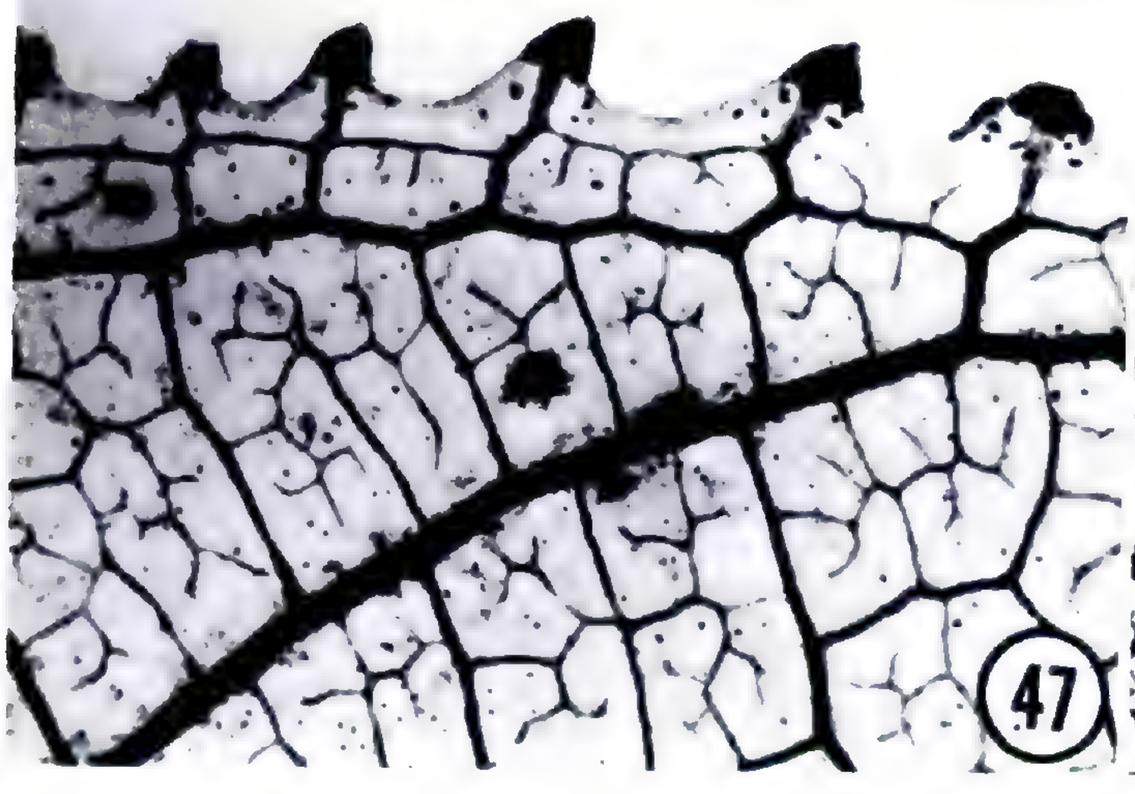
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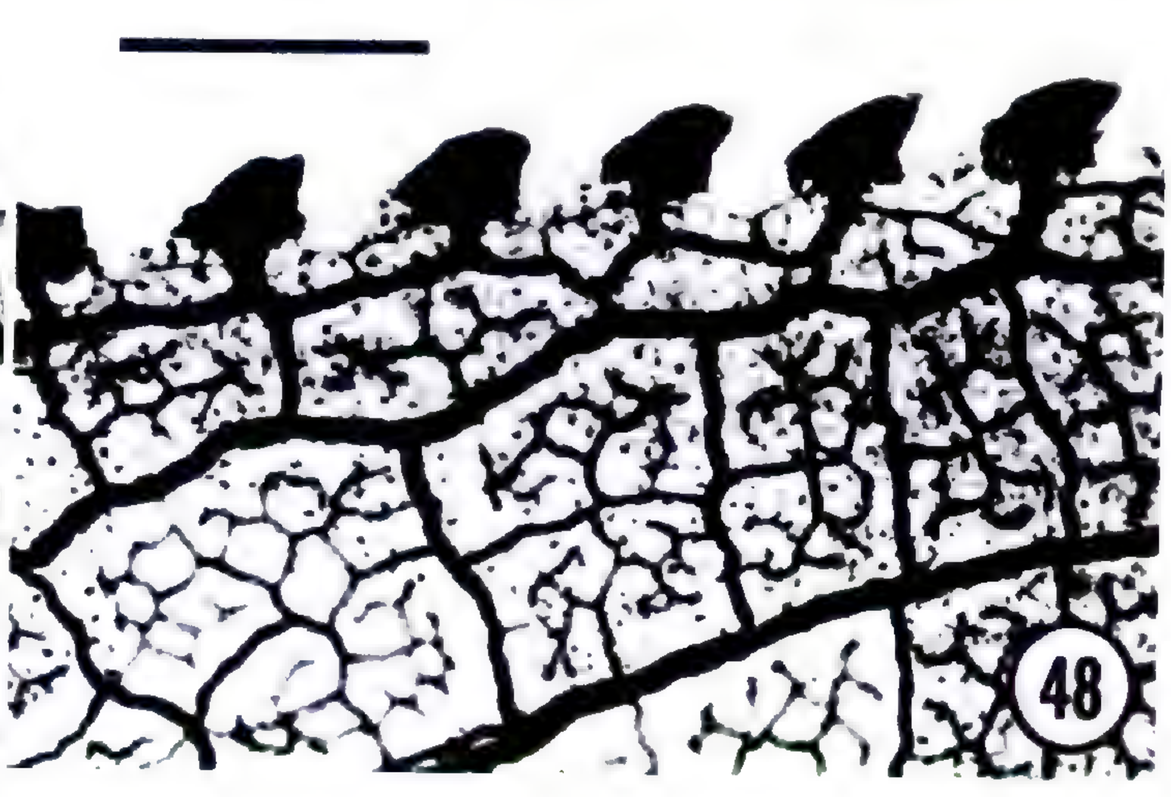
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closely to these early leaves, the secondary veins tend to be widely spaced, are never narrowly spaced, and form irregularly shaped intercostal areas. Beyond this observation, there is no established polarity regarding the spacing of secondaries. Possible ranalian outgroups give conflicting evidence. Leaves with few, widely spaced secondaries occur in the Amborellaceae and Austrobaileyaceae while leaves with numerous, closely spaced secondaries are found in Trimeniaceae, Winteraceae, Degeneriaceae, and Eupomatiaceae (G. Upchurch, pers. comm.).

Transitional secondary venation patterns are common and there is too little comparative information to polarize the character states with confidence. Prominent secondary arches occur and often tertiary and higher order loops form between the secondary arches and the margin (e.g., *Sarcandra glabra* (Figs. 1, 2), *Ascarina lucida* (Fig. 3), and *A. rubricaulis* (Fig. 6)). Higher rank leaves have a higher number of secondaries, and brochidodromy tends toward eucamptodromy at the proximal end of the leaf (e.g., *Hedyosmum grisebachii* (Fig. 10), *H. costaricense* (Fig. 16), *H. racemosum* (Fig. 17), *H. mexicanum* (Fig. 19), *H. bonplandianum* (Fig. 20)).

The semicraspedodromous pattern is seen where the tooth vein originates prominently from secondary arches of the brochidodromous plan as seen in *Sarcandra glabra* (Figs. 1, 2), *Ascarina philippinensis* (Fig. 4), *Chloranthus spicatus* (Fig. 5), and *Hedyosmum nutans* (Fig. 9). In Hickey & Wolfe's (1975) taxonomic review, semicraspedodromous leaves show up for the first time in the dilleniid genera, a group parallel to and slightly higher than the magnoliids. We have seen no previous discussion relating this patten closely to the brochidodromous leaves and yet it is found among genera in the Chloranthaceae that on other grounds are more primitive than *Hedyosmum*. Lorence (1985) included a survey of the leaf architecture in his monograph of the relict genera of the Monimiaceae of the Malagasy region. The patterns illustrated are mostly brochidodromous but include admixtures of craspedodromous patterns in *Ephippiandra madagarcariensis* and *Tambourissa ficus*, and semicraspedodromous in *E. tsaratanensis* and *T. trichophylla*. It appears to us that the developmental and phylogenetic relationships between brochidodromous and semicraspedodromous leaves are quite close and need to be adequately analyzed. Existing concepts should be regarded as tentative at this point but we suggest that the semicraspedodromous leaf type is one of, if not the earliest, associated with toothed leaves. The fact that many early ranalian leaves are entire-margined may have helped to obscure this relationship.

Fully eucamptodromous leaves can be seen in *H. goudotianum* (Fig. 21), *H. steinii* (Fig. 25), and *H. anisodorum* (Fig. 27). Some forms of eucamptodromous leaves (e.g., *H. gentryi* (Fig. 11), *H. neblinae* (Fig. 13), *H. arborescens* (Fig. 15)) have secondary arches tending to become straightened into an intramarginal vein. Without direct evidence, but because of the common association of brochidodromous and eucamptodromous venation patterns, we hypothesize that eucamptodromy is derived from an earlier brochidodromous prototype through a shift in ontogeny.

The large majority of leaves in this family are elliptic (narrowly elliptic with a length/width ratio of 4.3:1 to widely elliptic with a length/width ratio of 1.4:1). Leaves may be ovate (Fig. 1, *Sarcandra glabra*) or obovate (*Hedyosmum cuatrecazanum* (Fig. 38) and *H. peruvianum* (Fig. 39)). In most cases the tip is acuminate and the base cuneate or decurrent. Leaf size ranges from 10 to 300 mm and length and width seem tightly correlated as seen in Figure 49.

In the scatter plots (Fig. 49), the largest leaves (*Hedyosmum sprucei, H. anisodorum, H. strigosum, H. pungens, H. peruvianum*) occur in low to mid elevations in the Andes and Central America, whereas species with the smallest leaves (*H. domingense, H. pseudoandromeda, H. burgerianum, H. cumbalense*) are found on exposed ridgetops or high elevations. Species with leaves representing the central values of the scatter plots have a variety of habitat preferences that show no ready correlation.

Teeth in this family had been referred to by Hickey & Wolfe (1975) as chloranthoid, and Hickey & Taylor (1989) regard that type as prototypical for the angiosperms. However, we have noted that the leaf teeth in this family are quite variable and difficult to ascribe to one familial type (see

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FIGURES 41–48. Leaf tooth types. Cleared leaves of *Hedyosmum* and *Sarcandra*.—41. *H. scabrum*, type 1a.—42. *H. cumbalense*, type 1b.—43. *H. gentryi*, type 2a.—44. *H. arborescens*, type 2b.—45. *Sarcandra glabra* subsp. *glabra*, type 2b.—46. *S. glabra* subsp. *brachystachys*, type 2c.—47. *H. anisodorum*, type 3.—48. *H. spectabile*, type 3. Scale line = 2 mm.

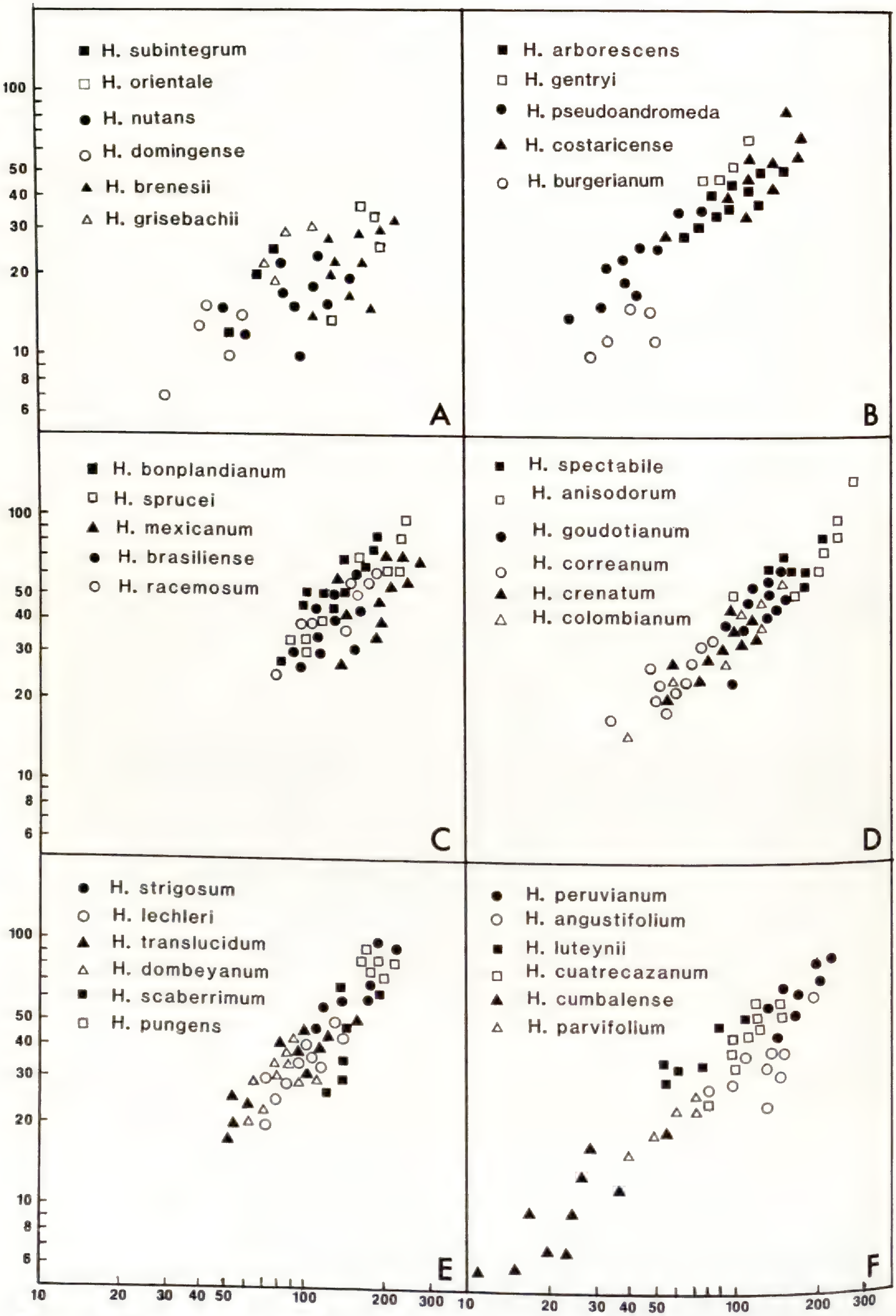

FIGURE 49. *Hedyosmum* leaf length (x axis) and width (y axis) in mm. Log scales. Up to ten specimens, when available, were used in each species sample.

Figs. 41–48). We categorized the leaf teeth of the Chloranthaceae as follows: type 1a (Fig. 41) is a broad tooth with a median vein usually arising from a secondary vein; it is symmetrically disposed between two smaller lateral and marginal converging veins. The three veins end in a vascular plexus distal to which appears a hydathodal glandular tip. On at least one specimen (*Chloranthus* sp.) a large stomate was noted on the surface of the tooth apex. Tooth type 1b (Fig. 42) still has the symmetrically converging lateral veins, but the tooth itself is shallow with only a small glandular tip protruding. Teeth of several species (*Hedyosmum grisebachii*, *H. subintegrum*, *H. nutans*, and *H. sprucei*) are not clearly placed into either type 1a or type 1b and are therefore coded simply as type 1 (Table 2). All the remaining teeth tend to have tips strongly curved toward the distal end of the leaf. The tooth apex is often oriented very close to the distal margin of the sinus. Type 2a (Fig. 43) has the median vascular bundle fused some distance back from the apex of the vascular plexus to the exmedial marginal vein. The admedial lateral becomes a marginal vein following around the sinus. The admedial lateral enters the tooth near the tip of the vascular plexus. In type 2b (Figs. 44, 45) the medial vein and the exmedial vein are fused far back from the tooth apex, and the admedial lateral follows the same path as the previous type. The unique feature is that the vascular plexus extends a greater distance into the attenuate leaf tooth. In type 2c (Fig. 46) the medial vein enters into the tooth with one small lateral vein merging far back from the tooth tip. The pattern is variable. There can be admedial, exmedial, or no lateral veins converging. Type 3 teeth (Figs. 47, 48) have a prominent densely sclerotic tip. They are vascularized by a prominent median vein with 0 to 2 converging lateral veins well inside the leaf margin. The nature of the teeth is currently being examined histologically. It is unclear at this point as to what exactly characterizes a chloranthoid tooth, if in fact, such a generalization can be made.

Since data are available for 37 of the 40 species of *Hedyosmum*, relationships within that genus can be discussed in greater detail. Specific architectural features support Todzia's (1988) classification, which recognizes two subgenera and five sections (Table 1). Leaves within subg. *Hedyosmum* all are lanceolate to narrowly elliptic with length/width ratios ranging from 10:1 to 3.3:1. Leaves in the 31 species of subg. *Tafalla* represented in our sample are mostly elliptic, with only a few species having obovate or lanceolate leaves. The length/width ratios of subg. *Tafalla* range mostly from 1.7 to 3.3:1 with a few exceptions (*H. brasiliense*, 3.6:1; *H. mexicanum*, 3.9:1; *H. scaberrimum*, 3.9:1; *H. angustifolium*, 4.1:1).

The median leaf rank differs among sections of the two subgenera presently recognized in *Hedyosmum*. Section *Orientale* and sect. *Hedyosmum* of subgenus *Hedyosmum* have median leaf ranks of $2r^1$ and $2r^{1.5}$ respectively, while sects. *Microcarpa*, *Macrocarpa*, and *Artocarpoides* of subg. *Tafalla* have higher median leaf rank ($2r^2$, $2r^3$, $2r^3$ respectively). Within sect. *Orientale* the species with the lowest leaf rank order, *H. orientale* ($2r^0$), is clearly the most primitive species in that group. This agrees with Hickey & Taylor's (1989) description of early angiosperm leaves that have very low rank. Within each section of *Hedyosmum*, however, leaf rank varies widely among species. Although the phylogeny within sect. *Microcarpa* is still in question (Todzia, 1988), rank may be indicative of species relationships. For example, the following species pairs are more closely related to each other than to other species within sect. *Microcarpa*, and each pair possesses the same leaf rank: *H. gentryi* and *H. neblinae* ($2r^3$); *H. costaricense* and *H. burgerianum* ($2r^2$); *H. racemosum* and *H. sprucei* ($3r^1$); *H. correanum* and *H. colombianum* ($2r^1$); and *H. goudotianum* and *H. spectabile* ($4r^0$).

Within *Hedyosmum* all tooth types are present except for type 2C. Section *Microcarpa* has the most varied array, including 1A, 1B, 2A, 2B, and 3. Species with type 3 teeth (*H. goudotianum*, *H. correanum*, *H. anisodorum*, *H. steinii*, *H. spectabile*, *H. scaberrimum*, and *H. translucidum*) appear quite closely related. *Hedyosmum burgerianum* and *H. costaricense* appear to be closely related by virtue of their widely spaced teeth. Considering its size, sect. *Macrocarpa* has the most limited range of all the groups with types 1A and 1B predominant and only one instance of type 2A, in *H. parvifolium*. In subg. *Hedyosmum*, sect. *Hedyosmum* and sect. *Orientale* have 1A, 1B, 2A, and 2B type teeth.

An intramarginal vein is present in only a few species, *H. pseudoandromeda* (Fig. 12), *H. gentryi* (Fig. 11), *H. neblinae* (Fig. 13), *H. arborescens* (Fig. 15), and *H. costaricense* (Fig. 16), and appears to be one of the defining characters of this group within the large sect. *Microcarpa*. Within sect. *Macrocarpa* distance between secondary veins appears to be a useful character. Closely spaced secondaries are present in *H. parvifolium* (Fig. 35), *H. cumbalense* (Fig. 36), *H. cuatrecazanum* (Fig. 38), *H. peruvianum* (Fig. 39), and *H. luteynii* (Fig. 40). These species are more closely related

to each other than to *H. angustifolium* (Fig. 37) and *H. scabrum* (Fig. 34) which, in addition to having more widely spaced secondary veins, also have a different pistillate inflorescence morphology.

Within *Hedyosmum* leaf architectural data do not appear to be correlated with elevation.

INTERGENERIC RELATIONSHIPS

Sarcandra, *Ascarina*, and *Chloranthus* all appear to have less well organized leaves than *Hedyosmum*. *Sarcandra* and *Chloranthus* leaves have widely spaced secondaries with poorly organized loops and unpredictable eucamptodromous patterns. *Ascarina lucida* has a primitive looping pattern and semicraspedodromous tooth vascularization. The teeth of leaves of all three genera are well vascularized.

There is some resemblance between these three genera and *Hedyosmum subintegrum* and *H. brasiliense*. *Hedyosmum brasiliense* in particular has anastomosing tertiaries. That is, the exmedial tertiary of the distal secondary fuses with the admedial tertiary of the next most basal secondary to form a craspedodromous vein that follows the course of other secondaries toward the margin.

In general, all *Hedyosmum* species examined have well-organized secondaries, good areolation, high leaf rank, reduced teeth, and close secondary spacing. It is the only genus that has developed intramarginal veins and specialized crystal patterns.

All four genera have teeth within the same size range and vascularization having the same brochidodromous/eucamptodromous series. All leaves have generally decurrent basal laminas, acute to acuminate tips, and tertiaries that seldom form predictable patterns.

INTERFAMILIAL RELATIONSHIPS

Little detailed information on leaf architecture of other ranalian families is available, but we do have a well-illustrated guide to the Lauraceae (Klucking, 1987) and the Annonaceae (Klucking, 1986). Lorence (1985) illustrated leaf clearings of species of Monimiaceae from the Madagascar region. An analysis of these works shows a number of similarities with the Chloranthaceae and a number of features that emphasize their lack of a close relationship.

The Lauraceae generally resemble the Chloranthaceae in having decurrent leaf bases, attenuate leaf tips, ovate leaf shape, and irregularly spaced secondary veins. Other resemblances are found among only some genera, and often only in certain species of these genera. These similarities include irregularly spaced, looped brochidodromous secondaries (*Licaria*, *Litsea*, *Aiouea*, *Aniba*); variable spacing and frequency of secondaries (*Nectandra*, *Ocotea*); forked secondaries (*Beilschmiedia*); eucamptodromous secondaries (*Cryptocarya*); and tendencies toward intramarginal veins (*Nothophoebe*, *Ocotea*).

Major differences from the Chloranthaceae include entire margins in all lauraceous genera, the presence of lateral primary veins in some species, the presence of often orthogonal tertiaries, a strong tendency toward percurrent tertiaries (*Actonoraphe*, *Alseodaphne*, *Beilschmiedia*, *Cinnamomum*, *Cryptocarya*, *Litsea*, *Mezilaurus*, and *Nectandra*). Admedial vein endings of several orders are found in *Beilschmiedia*. Ascending acrodromous secondaries are found in *Cinnamomum*, *Cryptocarya*, *Lindera*, *Neocinnamomum*, and *Neolitsea*. The synapomorphies found in the Lauraceae indicate an ancient separation between the two families.

While most phylogeneticists classify the Trimeniaceae with the Lauraceae, away from the Piperales (Cronquist, 1981; Takhtajan, 1987), Endress (1987) has called attention to numerous similarities between the Chloranthaceae and their proposed closest relatives, the Trimeniaceae. We compared specimens of *Trimenia* from the herbarium of the Missouri Botanical Garden, but specimens of *Piptocalyx* were not available. *Trimenia neocaledonica* Baker f. from New Caledonia has an entire-margined elliptic leaf of first leaf rank with a well-developed intramarginal vein. Secondary veins, averaging nine on each side of the midrib, are often branched, giving the secondaries a cladodromous appearance. This leaf shows little resemblance to any we examined in the Chloranthaceae. *Trimenia papuana* Ridl. from Papua, New Guinea, has a toothed elliptic leaf with about 28, often bifid secondaries per side. They are regular in arrangement, and therefore at least second rank order, with one intersecondary usually found per intercostal area. The secondaries end short of the margin at an undulating intramarginal vein, which follows the outline of the tooth lobes and shallow sinuses. Veins leave the intramarginal vein in a semicraspedodromous pattern and appeared to run to the base of the sinuses just distal to the tooth. The tooth has a glandular apiculus not characteristic of any seen in the Chloranthaceae. *Trimenia* tooth architecture of our specimens does not seem to fit any of the chloranthoid types that we have identified. However, Endress (1987, fig. 191) illustrated a cleared

tooth of the *T. papuana*, which we would interpret as similar to our type 3 chloranthoid type.

The opposite phyllotaxy and leaf base morphology of *Trimenia* are suggestive of the Chloranthaceae, and in both families tooth vascularization always seems to arise from brochidodromous loops or collectors and never from secondaries directly. In other ways they are quite distinguishable. In the Chloranthaceae, the main tooth vascularization is always direct and never by way of the sinus. No eucamptodromous or brochidodromous patterns were found in the *Trimenia* specimens examined.

In our limited observations of *Trimenia*, its leaves appear to have specialized independently and to a somewhat higher level than most Chloranthaceae. However, the postulated close relationship is not negated by our evidence.

Lorence's (1985) study of the Malagasy Monimiaceae reveals characters in those Lauralian genera that closely resemble characters found in the leaves of Chloranthaceae. Second rank, festooned brochidodromous leaves are found in *Monimia* and *Decaryodendron* with eucamptodromy found in *M. ovalifolia*. Widely spaced secondaries in craspedodromous or semicraspedodromous leaves are found in *Ephippiandra* and *Tambourissa*. Margins range from entire to dentate in the family. Dentate leaves are noted in *Hortenia* and *Tambourissa* but they have monimioid vascularization. That type does not resemble the Chloranthaceae in that the median vein servicing a tooth supports loops on both sides, which decrease in size toward the margin and tooth apex. In *Tambourissa*, species with entire adult leaves have dentate juvenile leaves. However close the two families are later judged to be, it is clear that they share the same grade or level of specialization of leaf architecture.

Klucking (1986) studied an extensive sample of the Annonaceae, which allows a detailed comparison with the Chloranthaceae. Again, it appears that the differences mitigate against postulating a close relationship.

Similarities between the Chloranthaceae and the Annonaceae include an ovate to elliptic shape and usually eucamptodromous venation. Brochidodromous leaves are found in a few genera (*Mezzettia*, *Artabotrys*, and *Marsypopetalum*) but not commonly. Decurrent secondaries are found only in *Cleistopholis*. Attenuate leaf tips are common in most genera.

A few species from Klucking's illustrated Annonaceae sample bear a close resemblance to *Sarcandra* and have a generally low rank. These include *Annona reticulata* L., *Guatteria schomburgkiana* C. Martius, *Desmopsis mexicana* R. E. Fries, *Greenwayodendron suaveolens* Engl. & Diels, *Goniothalamus repevensis* Pierre, *Porcelia macrocarpa* (Warm.) Fries, *P. nitidifolia* Ruíz Lopez & Pavón, *Sageraea glabra* Merr., *Polyalthia subcordata* Blume, and *Oxandra riedeliana* R. E. Fries. These specimens do not come from geographically close localities but rather from the tropical range of the Annonaceae.

All of the specializations found in the Annonaceae represent trends not present in the Chloranthaceae. Among these are strongly percurrent tertiaries in most genera, the absence of teeth in all genera, close and regularly spaced secondaries, basal lamina insertion that is emarginate, blunt, incipiently cordate in species of *Friesodielsia*, *Dasymaschalon*, and *Ellipeia*; strongly ascending secondaries in *Platymitra*, *Mitrephora*, and *Kingstonia*, obovate shape in *Asimina*, and emarginate leaf tips in *Goniothalamus*.

Many more studies need to be made of ranalian families, especially among the genera having low rank leaves. Important early dicot trends are abundant among ranalian genera, but we have little understanding of the systematic significance of their leaf architecture.

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NOTES ON THE SYSTEMATICS OF *ARISTOLOCHIA* SUBSECT. *HEXANDRAE*[1]

Favio González G[2]

ABSTRACT

Using comparative morphology studies from 123 species of *Aristolochia* sect. *Gymnolobus* subsect. *Hexandrae*, this taxon is reevaluated. Two series (*Hexandrae* and *Thyrsicae*, ser. nov.) and two subseries (*Anthocaulicae*, ser. nov., and *Hexandrae*) are recognized. *Aristolochia* (*Thyrsicae*) *maxima* and *Aristolochia* (*Anthocaulicae*) *iquitensis* are designated as types.

The Aristolochiaceae are represented in America by the genera *Aristolochia*, *Asarum*, *Euglypha*, and *Holostylis*. The noteworthy diversity and wide distribution of *Aristolochia* (250 species ranging from ca. 40°N latitude to ca. 35°S latitude) contrasts with the restricted distributions of *Asarum* (southeastern and northwestern United States) and the monotypic genera *Euglypha* and *Holostylis* (central South America). Most New World species of *Aristolochia* belong to *Aristolochia* sect. *Gymnolobus* Duchartre (1854, 1864).

While working on a revision of *Aristolochia* in Colombia, I (González, 1989) studied the comparative morphology of the 27 species reported from this country, as well as another 96 neotropical species. All species belonged to *Aristolochia* sect. *Gymnolobus* Duchartre subsect. *Hexandrae* Duchartre (1854, 1864; lectotype here designated, *A. ringens* Vahl). Based on this study, it was possible to recognize two new series and two new subseries into that subsection.

The present treatment appears as an alternative to the classical works of the subsection made by Duchartre (1854, 1864), Masters (1875), Schmidt (1935), and Hoehne (1942). These authors considered the characters of the perigonium to be essential for grouping species; such characters are unstable, however, and suggest that convergence or parallelism have occurred (González, 1989).

The new series and subseries are recognized by the correlation of characters related to: abscission basal zone in the petiole, whose appearance is here reported for the first time in the Aristolochiaceae; typology of inflorescences; and morphology of capsule and seeds. The concepts and terminology used here to describe inflorescences were developed by Mora-Osejo (1987), Troll (1950, 1964, 1969), and Weberling (1981, 1983, 1985). These new concepts made it possible to establish the basic types of inflorescences in *Aristolochia* and to apply these types to the recognition of natural groups.

In order to increase the understanding of the following descriptions, a short explanation of unfamiliar concepts related to the inflorescence morphology is desirable. Holocaulic plants (sensu Mora-Osejo, 1987) have stem systems (holocaules) with high innovation (branching) capacity, with vegetative elements (i.e., bracts, buds, and leaves) included in the floriferous zone (Figs. 1, 2A, 3, 5A) or synflorescence (sensu Troll, 1950, 1964). In *Aristolochia*, the synflorescence is polytelic (lacking a terminal flower on the main axis or the lateral branches of various order); the growth of the shoots is indeterminate. The synflorescence is formed by the florescence (fl, distal floriferous unit of the polytelic main axis; Figs. 1, 3) and the coflorescences (cfl, florescences of the lateral branches, or paracladia, pc; Figs. 1, 3). The florescence and the coflorescences become equivalent to the anthotagma (sensu Mora-Osejo, 1987) or floriferous zone, subtended by a vegetative zone called hypotagma (sensu Troll, 1964); the hypotagma (hptg,

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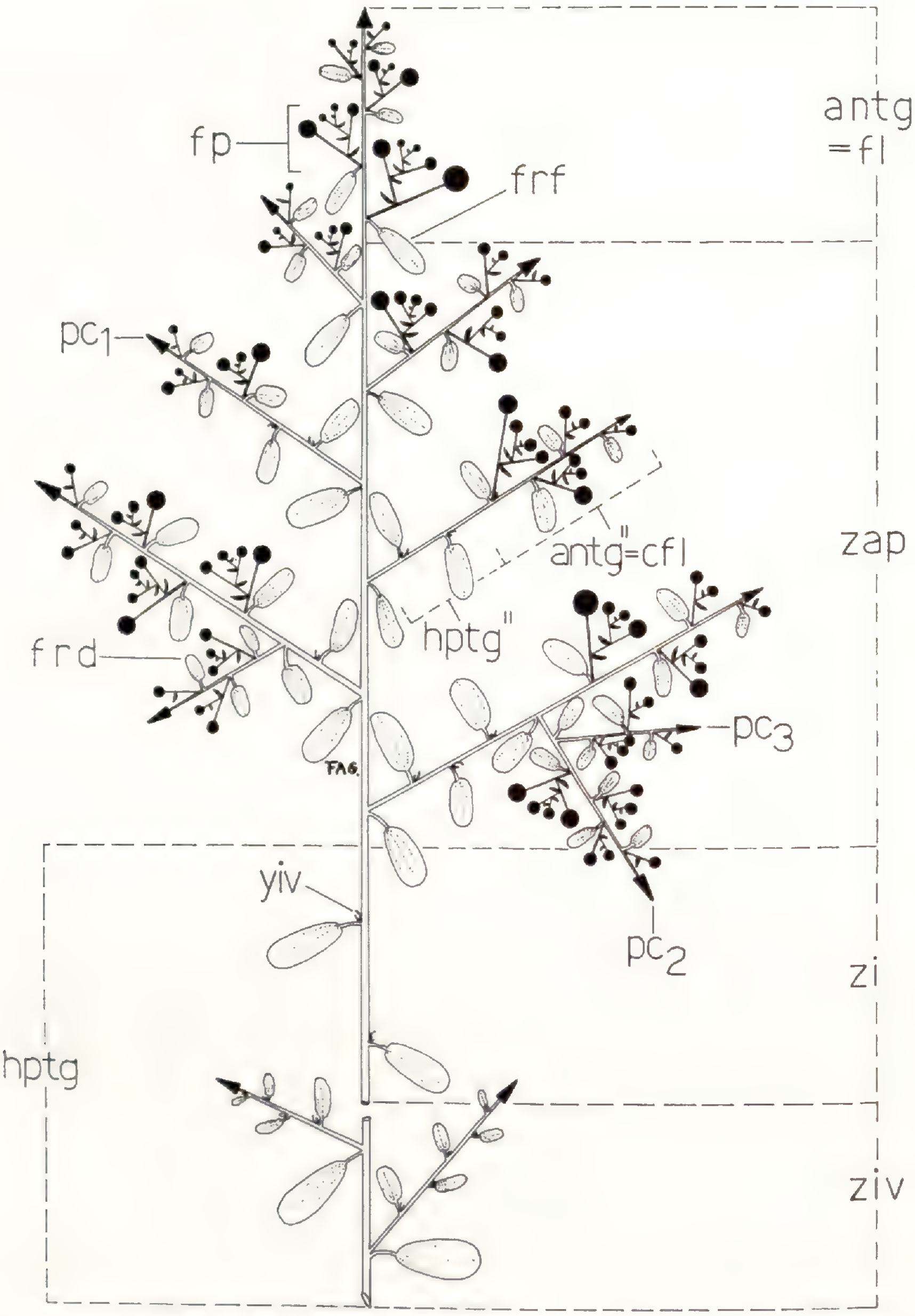

FIGURE 1. Diagram of a frondose, polytelic, thyrsoid holocaule, from *Aristolochia* ser. *Thyrsicae*; antg, anthotagma; cfl, coflorescence; fl, florescence; fp, partial florescence; frd, frondulose pherophyll; frf, frondose pherophyll; hptg, hypotagma; pc, paracladia of first (pc_1), second (pc_2) and third (pc_3) order; yiv, innovation bud; zap, anthoparacladial zone; zi, inhibition zone; ziv, enrichment or innovation zone.

Figs. 1, 3) includes the inhibition zone (zi) and the innovation zone (ziv).

In the species of *Aristolochia* ser. *Thyrsicae*, the partial florescences (ultimate elements of the florescence and the coflorescences) are rhipidia or helicoid cymes (Figs. 1, 2A, B); this implies that the synflorescence is thyrsoid. On the other hand, the synflorescence in the species of *Aristolochia* ser. *Hexandrae* subser. *Hexandrae* is racemose (botrytic) because each partial florescence is reduced to a terminal flower (Figs. 3, 5A, B). In both taxa the pherophylls (vegetative elements that subtend each partial florescence) are leaves, and the synflorescence is therefore frondose (frf, Figs. 1, 3); however, in some higher-order paracladia the pherophylls become frondulose (frd, Figs. 1, 3; sensu Weberling, 1981).

In contrast, the inflorescences in the anthocaulic species of *Aristolochia* subser. *Anthocaulicae* are restricted to lateral shoots called anthocaules (sensu Mora-Osejo, 1987); they tend to be strongly homogeneous and specialized for the reproductive function. Each shoot is a short paracladium; this implies that it is truncate and has indeterminate

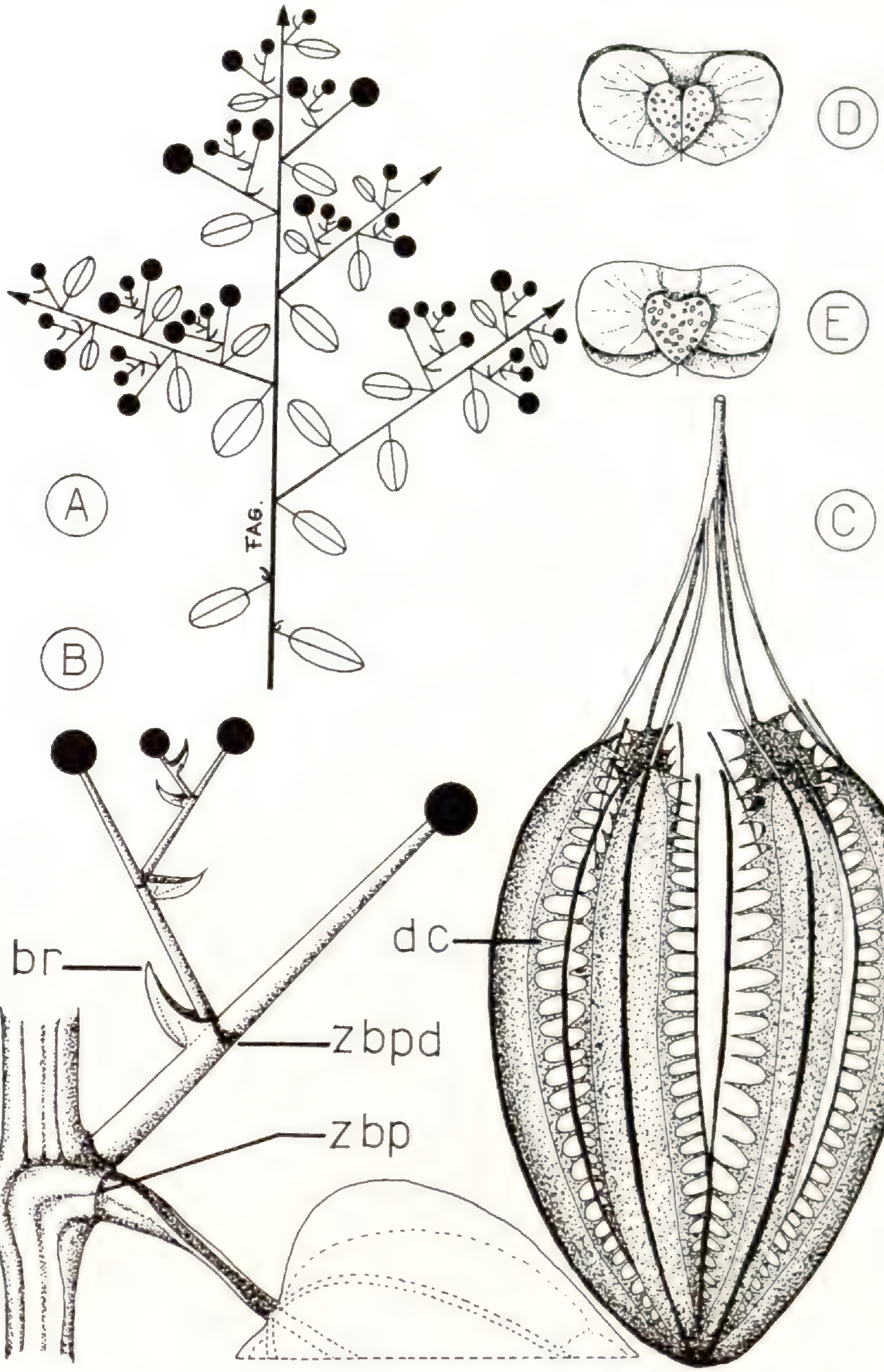

FIGURE 2. *Aristolochia* ser. *Thyrsicae*. Diagram of diagnostic characters.—A. Synflorescence.—B. Partial florescence; br, bracteole; zb, abscission basal zone of the petiole (zbp) and the peduncle (zbpd).—C. Capsule; dc, latticelike dissepiment. D, E. Seeds.—D. Adaxial view.—E. Abaxial view.

growth. Its vegetative impulse is not strong; its vegetative elements (buds, internodia, and leaves) are extremely reduced; the shoot is unbranched and is occupied totally by the coflorescence (the hypotagma disappears); these shoots correspond to the paracladial anthoblast model (sensu Mora-Osejo, 1987). These paracladia are restricted to a basal zone of the plant, here called the anthoparacladial zone (zap, Fig. 4). As in the species of *Aristolochia* subser. *Hexandrae*, these floriferous shoots are racemose, but each flower is subtended by a bracteal pherophyll (fb, Figs. 4, 5F, G).

The outline of the new taxonomic treatment here proposed is the following (the order of the taxa belongs with the typological derivation, discussed in González, 1989):

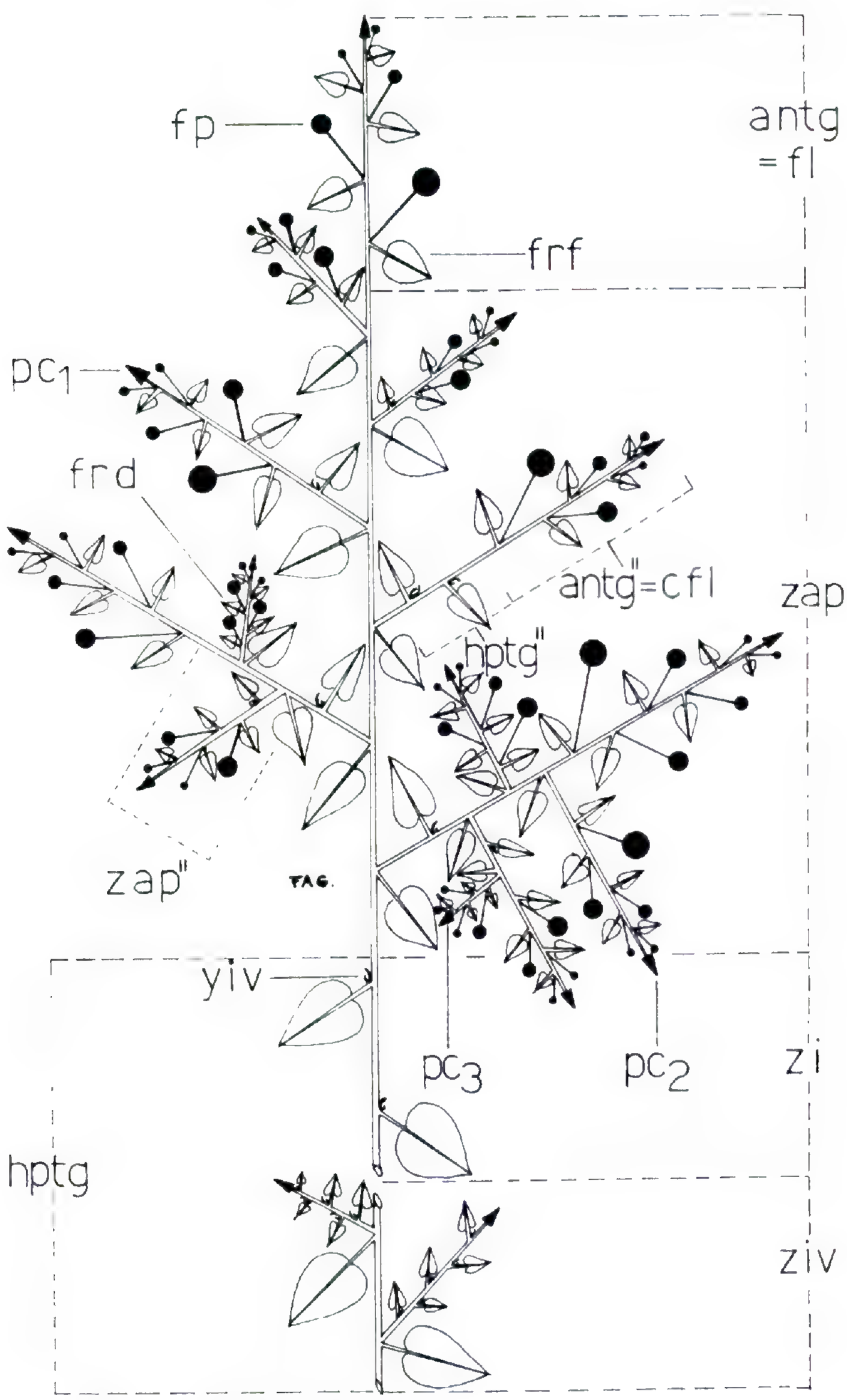

FIGURE 3. Diagram of a frondose, polytelic, racemose holocaule, from *Aristolochia* ser. *Hexandrae* subser. *Hexandrae*. (Abbreviations as in Fig. 1.)

Aristolochia subsect. *Hexandrae*
ser *Thyrsicae* ser. nov.
ser. *Hexandrae*
subser. *Hexandrae*
subser. *Anthocaulicae* subser. nov.

Aristolochia ser. **Thyrsicae** F. González, ser. nov. HOLOTYPE: *Aristolochia maxima* Jacq. Figures 1, 2.

Plantae holocaulicae, synflorescentia frondosa, thyrsica; paracladia interdum pseudocauliflora vel cauliflora, ad florescentiam partialem reducta; florescentiae partiales ripidiis vel cymis helicoidalibus conformatae. Flores bracteolati. Zona abscissionis basi petioli et pedunculi. Dissepimenta capsulae cancellata. Semina transversim oblonga, plana, bialata, ala abaxialis quam adaxialis brevior.

Holocaulic plants, synflorescence frondose, thyrsoid, paracladia sometimes pseudocauliflorous or cauliflorous and then reduced to a partial florescence; partial florescence a rhypidium or helicoid cyme; flowers bracteolate. Petiole and peduncule with basal abscission zone. Capsule with dissepiments latticelike. Seeds transverse-oblong, two-winged, abaxial wing shorter than adaxial.

Distribution: Neotropics (southern Mexico to Argentina).

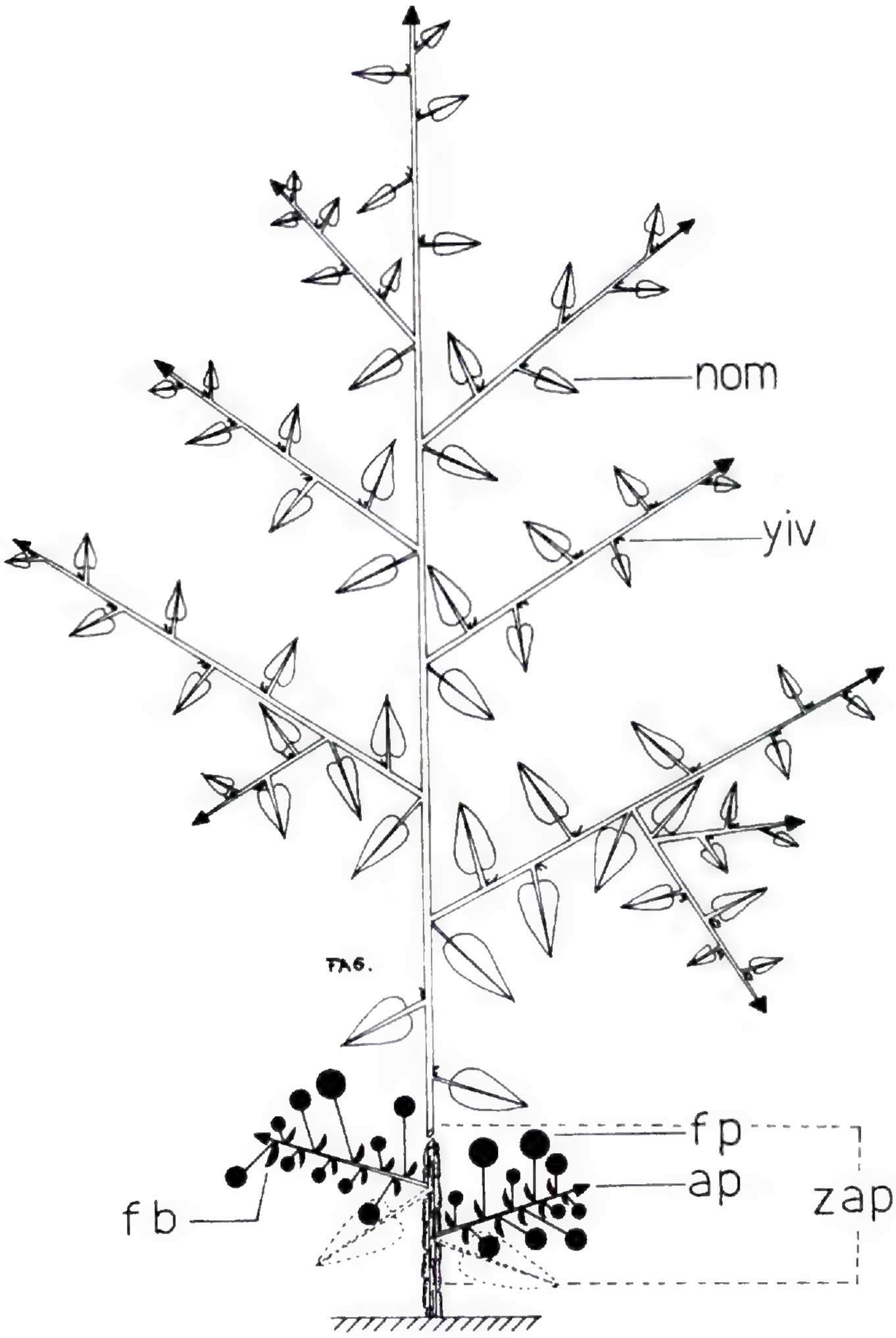

FIGURE 4. Diagram of an anthocaule from *Aristolochia* ser. *Hexandrae* subser. *Anthocaulicae*; ap, paracladial anthoblast; fb, bracteal pherophyll; fp, partial florescence; nom, nomophyll; yiv, vegetative innovation bud; zap, anthoparacladial zone.

The following species belong in *Aristolochia* ser. *Thyrsicae*: *A. acutifolia* Duchartre, *A. colossifolia* Hoehne, *A. mathewsii* Duchartre, *A. maxima* Jacq., *A. melastoma* Manso, *A. ovalifolia* Duchartre, *A. pannosoides* Hoehne, *A. pfeiferi* Barringer, *A. silvatica* Barb. Rodr., *A. sprucei* Mast., *A. tonduzii* Schmidt, *A. translucida* Pfeifer, and *A. trianae* Duchartre.

Aristolochia ser. **Hexandrae.** Figures 3–5.

Holocaulic or anthocaulic plants, synflorescence racemose; partial florescence reduced to the terminal flower. Flowers ebracteolate (except in *A. grandiflora*). Petiole and peduncle without basal abscission zone. Capsule dissepiments entire. Seeds rhomboid, ellipsoid, or from wide- to narrowly ovoid, unwinged or having one wing.

Into this series are recognized two subseries, described below.

Aristolochia ser. **Hexandrae** subser. **Hexandrae.** Figures 3, 5A–E.

Holocaulic plants; synflorescence with distal, frondose florescence and coflorescences; florescence and coflorescences sparsely flowered with elongate internodes, more than 1 cm long; pherophylls frondose, sometimes frondulose, petiolate, 10 mm long and ≥6 mm wide.

Distribution: Neotropics and adjacent subtropical, temperate areas; the highest density of species occurs in the Neotropics.

The species now recognized in *Aristolochia* ser. *Hexandrae* subser. *Hexandrae* are: *A. albertiana*

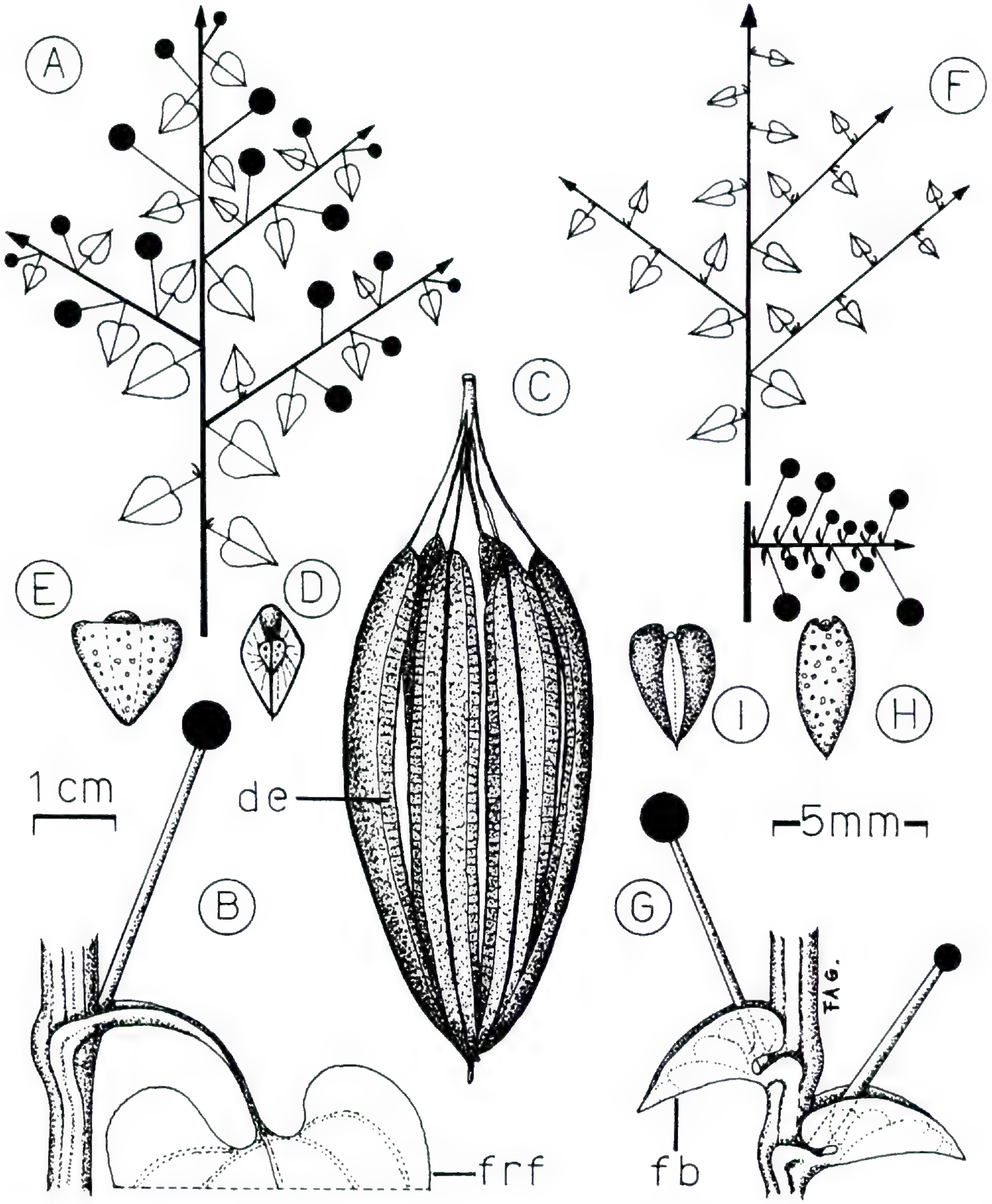

FIGURE 5. *Aristolochia* ser. *Hexandrae*. Diagram of diagnostic characters. A–E. *Aristolochia* ser. *Hexandrae* subser. *Hexandrae*.—A. Synflorescence.—B. Partial florescence at the axil of a frondose pherophyll (frf).—C. Capsule; de, entire dissepiment.—D. E. Seeds. F–I. *Aristolochia* ser. *Hexandrae* subser. *Anthocaulicae*.—F. Synflorescence.—G. Two partial florescences at the axil of one each bracteal pherophylls (fb).—H, I. Seeds (not to scale, except B and G).

Ahumada, *A. andahuaylensis* Ahumada, *A. anguicida* Jacq., *A. angustifolia* Cham., *A. arcuata* Mast., *A. argentina* Griseb., *A. barbouri* Barringer, *A. bilobata* L., *A. brasiliensis* Mart. & Zucc., *A. brevifolia* (Cham.) Haum., *A. burchellii* Mast., *A. burkartii* Ahumada, *A. cabrerae* Ahumada, *A. castellanosii* Ahumada, *A. caudata* Jacq., *A. ceresensis* Kuntze, *A. claussenii* Duchartre, *A. clavidenia* Griseb., *A. compta* Hoehne, *A. cordigera* Willd. ex Duchartre, *A. curviflora* Malme, *A. cymbifera* Mart. & Zucc., *A. chachapoyensis* Ahumada, *A. chilensis* Miers, *A. deltoidea* HBK, *A. didyma* S. Moore, *A. ehrenbergiana* Cham., *A. ekmanii* Schmidt, *A. elegans* Mast., *A. eriantha* Mart. & Zucc., *A. esperanzae* Kuntze, *A. fimbriata* Cham., *A. fuertesii* Urb., *A. gabrielis* Du-

chartre ex Briq., *A. galeata* Mart. & Zucc., *A. gehrtii* Hoehne, *A. gibertii* J.D. Hook., *A. gigantea* Mart. & Zucc., *A. ginzbergeri* Ahumada, *A. glandulosa* J. Kickz fil., *A. glossa* Pfeifer, *A. grandiflora* Sw., *A. guianensis* Poncy, *A. haitensis* Ekman & Schmidt, *A. hatschbachii* Ahumada, *A. hians* Willd., *A. hutchisonii* Ahumada, *A. hypoglauca* Kuhlm., *A. inflata* HBK, *A. killipiana* Schmidt, *A. labiata* Willd., *A. leptosticta* Urb., *A. lindeniana* Duchartre, *A. lingua* Malme, *A. lingulata* Ule, *A. loefgrenii* Hoehne, *A. macrorrhyncha* Hoehne, *A. macrota* Duchartre, *A. malmeana* Hoehne, *A. manaosensis* Ahumada, *A. marianensis* Ahumada, *A. melanoglossa* Speg., *A. mishuyacensis* Schmidt, *A. mossii* S. Moore, *A. nummularifolia* HBK, *A. odoratissima* L., *A. orbicularis* Duchartre, *A. papillaris* Mast., *A. passifloraefolia* A. Rich., *A. paulistana* Hoehne, *A. peltata* L., *A. peltato-deltoidea* Hoehne, *A. physodes* Ule, *A. pilosa* HBK, *A. pohliana* Duchartre, *A. prostrata* Duchartre, *A. pubescens* Willd., *A. pucarensis* Ahumada, *A. raja* Mart. & Zucc., *A. ringens* Vahl, *A. rugosa* Lam., *A. rumicifolia* Mart. & Zucc., *A. schreiteri* Ahumada, *A. schultzeana* Schmidt, *A. schulzii* Ahumada, *A. smilacina* (Klotzsch) Duchartre, *A. stomachoides* Hoehne, *A. taliscana* Hook. & Arn., *A. tentacula-ta* Schmidt, *A. tigrina* A. Rich., *A. triangularis* Cham., *A. trilobata* L., *A. truncata* Fielding & Gardner, *A. urupaensis* Hoehne, *A. xerophytica* R. E. Schultes, *A. warmingii* Mast., and *A. weddellii* Duchartre.

Aristolochia ser. **Hexandrae** subser. **Anthocaulicae** F. González, subser. nov. HOLOTYPE: *Aristolochia iquitensis* Schmidt. Figures 4, 5F–I.

Plantae anthocaulicae; synflorescentia truncata, ad anthoblastos paracladiales, pseudocaulifloros vel caulifloros bracteosos reducta; anthoblasti paracladiales ad coflorescentiam saepe confertifloram reducti; internodia coflorescentiae constricta, ad 1 cm longa. Phorophylla bracteosa sessilia vel subsessilia, usque ad 7 mm longa et 4 mm lata.

Anthocaulic plants; synflorescence reduced to paracladial anthoblasts, pseudocauliflorous or cauliflorous, bracteate; paracladial anthoblasts reduced to the coflorescence (hypotagma absent), usually densely flowered, the internodes constricted, to 1 cm long; pherophylls bracteal, sessile or subsessile, to 7 mm long and 4 mm wide.

Distribution: Primary, wet tropical forests, especially the Amazon basin.

The following species are recognized in this subseries: *Aristolochia bukuti* Poncy, *A. cauliflora* Ule, *A. cordiflora* Mutis ex HBK, *A. cornuta* Mast., *A. cremersii* Poncy, *A. flava* Poncy, *A. goudotii* Duchartre, *A. guentheri* Schmidt, *A. iquitensis* Schmidt, *A. klugii* Schmidt, *A. lagesiana* Ule, *A. leuconeura* Linden, and *A. ruiziana* Duchartre.

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CALYDOREA HERBERT (IRIDACEAE–TIGRIDIEAE): NOTES ON THIS NEW WORLD GENUS AND REDUCTION TO SYNONYMY OF *SALPINGOSTYLIS*, *CARDIOSTIGMA*, *ITYSA*, AND *CATILA*[1]

Peter Goldblatt[2] *and*
James E. Henrich[3]

Abstract

Subequal tepals spreading from the base, free stamens, and short slender style branches with simple, obtuse to emarginate apices, the defining generic criteria for the southern South American *Calydorea* (Iridaceae–Tigridieae) (Herbert, 1843a) also characterize the Florida (U.S.A.) monotypic *Salpingostylis* (Small, 1931), the Mexican *Cardiostigma* (Baker, 1876), and the Venezuelan *Itysa* Ravenna (1986). *Salpingostylis* and *Cardiostigma* hardly differ from one another and are congeneric; they can be distinguished from *Calydorea* only by their secund flower, weakly eccentric style that divides near the apex of the anthers, and short style branches. *Itysa* also has secund flowers with spreading subequal tepals, free stamens and slender, simple style branches. It is unusual only in having the anthers coherent at their bases and a style that divides above the level of the anthers. Typical *Calydorea* has upright flowers and a central style that divides near the bases of the anthers into relatively longer style branches that twist weakly so that they come to lie between, rather than opposite, the style branches. We consider the differences between *Calydorea*, *Cardiostigma*, *Salpingostylis*, and *Itysa* too insignificant to merit generic segregation and unite them all under *Calydorea*. An unusual species of *Calydorea*, *C. pallens*, which has unequal inner and outer tepals and style branches that lie opposite the anthers, is strikingly similar to *Catila amabilis* (Ravenna, 1983), the latter having somewhat larger and more intensely colored flowers, the anthers of which clasp the style branches after anthesis. These two species belong in the same genus, and we recommend treating both as *Calydorea* in which we consider them to be relatively unspecialized. Other members of Tigridieae, notably *Onira*, *Eleutherine*, and *Gelasine*, that have free stamens and simple style branches are considered in relation to *Calydorea*. The phylogenetic position of the species or species clusters of *Calydorea* are analyzed cladistically and are discussed in relation to other taxa of Tigridieae and the basic character states of the tribe and its sister taxon Mariceae.

Described in 1843 by the British botanist William Herbert, *Calydorea* was erected to include a species of bulbous and plicate-leafed Iridaceae from Chile, *Sisyrinchium speciosum*, which was misplaced in *Sisyrinchium*. Two features distinguished *Calydorea* from other genera of Iridaceae then known that also had a bulbous rootstock and plicate leaves, and the same basic vegetative morphology: free stamens; and a style with long, slender, undivided branches loosely alternating with the stamens.

By 1843, 11 genera with similar vegetative morphology had already been described, and more than 15 additional ones have since been added. Except for some obvious synonyms, each differed largely in its floral morphology and was characterized by unusual stamen and/or stylar specializations, and sometimes by differences in the relative size and shape of the inner and outer tepal whorls. The bulbous and plicate-leafed genera of Iridaceae are now treated as members of Tigridieae, one of four tribes (Goldblatt, 1990) of Iridoideae, the others being Sisyrinchieae, Irideae, and Mariceae. Iridoideae is the only one of the

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four subfamilies of Iridaceae that occurs in the New World (Goldblatt, 1982, 1990). A notable feature of Tigridieae (Figs. 1, 2) is the unusual degree of variability in the style branches, which frequently form a highly specialized and complex structure, intimately associated with the stamens, which are also sometimes specialized. This contrasts markedly with the vegetative uniformity in the tribe.

More than 25 genera of plicate-leafed Iridaceae with bulbs have been described, and all but a few of these appear to be very weakly founded. They are largely based on trivial differences in style or stamen structure. Compared with Iridaceae–Iridoideae in Africa and Eurasia, the generic limits of the Tigridieae seem too finely drawn, and it seems timely to attempt to reduce some of the genera that differ so little from each other. Not only is some degree of consistency in the criteria for recognition of genera desirable at least within the family, but there is a need to define the New World genera of Iridaceae so that usable keys and descriptions can be written. *Cardiostigma* Baker (1876), *Salpingostylis* Small (1931), *Catila* Ravenna (1983), and *Itysa* Ravenna (1986) are four such examples of weakly defined genera, and they are reduced to synonymy in *Calydorea* here. Also critically considered in relation to *Calydorea* are *Gelasine*, *Onira*, and *Eleutherine*, which are at least partly defined by, or contain species with, slender, undivided style branches.

Cardiostigma

Based on the southern Mexican *C. longispathum* (Klatt) Baker, *Cardiostigma* (Baker, 1876: 102) was reduced to synonymy in *Sphenostigma* Baker (1876: 124) by Bentham & Hooker (1883) soon after it was described. The latter is founded on the Brazilian *S. sellowianum* (Klatt) Baker. Baker (1892) expanded *Sphenostigma* to include 11 species, and Foster (1945) added three more. Ravenna (1977) has, however, made a convincing argument for transferring the type of *Sphenostigma*, but not other members of the genus, to *Gelasine*, in which it is now known by an earlier synonym, *G. coerulea* (Vellozo) Ravenna. With *Sphenostigma* thus included in *Gelasine*, Ravenna (1977, 1979, 1986) transferred most of the erstwhile species of that genus to *Ennealophus* N.E. Br., *Phalocallis*, *Cardiostigma*, and the new genera *Ainea* and *Lethia*. One species that Ravenna has not dealt with to date is *Sphenostigma coelestinum* (= *Salpingostylis coelestinum*), and this is discussed in detail below.

Cardiostigma sensu Ravenna comprises three species, *C. longispathum* (the type), *C. mexicanum* (R. Foster) Ravenna, and *C. hintonii* (R. Foster) Ravenna. Ravenna never explained his concept of *Cardiostigma*, but its only notable feature seems to be its flower. This is secund and consists of a blue perianth of subequal spreading tepals, not clearly divided into a limb and claw and without perigonal nectaries; free stamens; and a slender, eccentric style with three short, simple branches. This at least applies to *C. longispathum* and *C. mexicanum*. In *C. hintonii* the three well-defined style branches are each deeply forked for about two-thirds of their length. This style corresponds exactly to that of *Ainea* (Ravenna, 1979) and *Alophia* (Herbert, 1840), and we assume that it is related to these genera rather than to the other species of *Cardiostigma*. We will not deal further with *C. hintonii* here.

Salpingostylis

This genus is monotypic, containing only the Florida species *Salpingostylis coelestinum* (basionym *Ixia coelestina* Bart.), which was, as recently as 1974, regarded as a not particularly unusual member of *Sphenostigma* (Goldblatt, 1974). Small (1931) described *Salpingostylis* and regarded it as monotypic, but his opinion was largely ignored (Foster, 1945; Goldblatt, 1974). Only after 1977, when Ravenna reduced *Sphenostigma* to synonymy in *Gelasine*, has *Salpingostylis*, more or less by default, been recognized.

A careful comparison of the available collections of *Salpingostylis* and *Cardiostigma* sensu Ravenna leaves us in no doubt that, with the exception of *C. hintonii* (mentioned above), these are congeneric. *Salpingostylis coelestinum* has the identical flower described above for *C. longispathum* and *C. mexicanum*, secund in orientation with subequal tepals, free stamens, and a long style. Examination of ample herbarium material and some accompanying illustrations made from live plants also makes it clear that the style is divided into distinct branches, not obscurely lobed as is sometimes thought (Fig. 1A). A reading of the literature and examination of living and preserved specimens have not indicated any reason to separate *Salpingostylis* and *Cardiostigma* from one another, and little to distinguish them from *Calydorea* (Fig. 1B).

Itysa

Described by Ravenna in 1986, *Itysa* comprises two species of northern South America. Both are broadly similar to *Calydorea* and *Cardiostigma* in

FIGURE 1. Flowers, style, and stamen detail and enlargement of style apex in species of *Calydorea*.—A. *C. coelestina* (*Salpingostylis*) (with habit).—B. *Calydorea* sp.—C. *C. gardneri* (*Itysa*).—D. *C. pallens*.—E. *C. amabilis* (*Catila*). Habit and flowers full size; stamens and style × 3; style branch apices much enlarged.

vegetative morphology, and they have secund flowers with subequal inner and outer tepals lacking differentiation into a limb and claw. The filaments are free, and the long style divides above the level of the anthers into three short, slender branches (Fig. 1C), the structure of which closely resembles that in *Calydorea*. One peculiarity of the genus is that the bases of the anthers are coherent around the style. Except for this unusual feature, both species of *Itysa* seem to correspond to the species of *Cardiostigma* in particular.

CALYDOREA

Flowers of *Cardiostigma*, *Salpingostylis*, and *Itysa* correspond closely to the type and most other

species of *Calydorea* (Fig. 1B) with the following differences. The flower is upright not secund, and the style is shorter, dividing opposite the base of the anthers. The style branches are thus comparatively longer and more slender, and by a weak twisting lie loosely between the anthers. (This is not a fundamental difference in the position of the ovary or style branches in relation to the stamens.) In *Salpingostylis* and *Cardiostigma*, the style divides just above the apex of the anthers and the exact position of the style branches relative to the anthers is obscured because the style is weakly eccentric (whether by design or the effect of gravity in the secund flower is not known) (Fig. 1A). However, the structure of the style and style branches of *Salpingostylis*, *Cardiostigma* sensu Ravenna, *Itysa*, and *Calydorea* is very similar (compare details of style arms in Fig. 1A–D).

As far as we can tell from live specimens of a *Calydorea* sp. from Argentina, and an illustration of the closely related *C. xiphioides* (Poeppig) Espin. (synonym *C. speciosa*), there are no other taxonomically significant differences between *Calydorea*, *Cardiostigma*, *Salpingostylis*, and *Itysa*. The secund flower, longer style, short style branches, and basally connate anthers are inadequate criteria on which to base genera in Iridoideae. Thus, as presently understood, *Cardiostigma*, *Salpingostylis*, and *Itysa* cannot be upheld and are here reduced to synonymy. The minor differences that we have outlined, in conjunction with the correlated geographic disjunction, appear to merit sectional separation within one genus at best. The necessary nomenclatural changes are presented below, together with short notes about each species.

Calydorea pallens and *Catila* Ravenna

When other species currently assigned to *Calydorea* are taken into account, the circumscription of the genus is somewhat expanded. In *C. pallens* Griseb., the style is shorter than in *C. xiphioides* and *Calydorea* sp., and the branches lie opposite the anthers, though not appressed to them (Fig. 1D); the tepals are weakly unguiculate; and the inner tepals are smaller than the outer. *Calydorea pallens* bears a remarkable resemblance to *Catila amabilis* Ravenna (Fig. 1E), the type and only species of *Catila* (Ravenna, 1983), which differs significantly from it only in having a larger flower with more strongly unguiculate tepals of a darker purple color and in the anthers being closely applied to the style branches. The inner tepals of *Catila* resemble many other *Tigridieae* in having the base of the limb folded back on itself and bearing a median zone of nectariferous tissue. There is no basis for the generic separation of *Calydorea pallens* and *Catila*.

Phylogenetic Considerations

The basic floral morphology in Tigridieae appears to be similar to the complex structure encountered in *Cypella* (e.g., Ravenna, 1981a, b), which is very similar to the basic flower of Mariceae (Fig. 2A), sister taxon of Tigridieae (Goldblatt, 1990). Here the tepals are clawed with the claws forming an open cup, and the inner tepals are smaller than the outer, each folded back on itself at the base of the limb, in which area there is a zone of nectaries surrounded by an area of contrasting coloration. The style branches are thickened and compressed, and terminate in a pair of flat appendages, called crests because of their resemblance to similar structures in *Iris*. The filaments are free, usually threadlike, and too weak to support the anthers, which are closely applied (not united) to the abaxial side of the style branch. The anthers usually reach to just below the stigma, a transverse band of tissue (Fig. 2A) at the base of the crests on the abaxial surface of the style branch. (The stigma may bear a pair of small appendages similar to the crests.)

This complex structure is thought to be basal (plesiomorphic) for a tribe in which much simpler stylar structures also occur (as in *Calydorea*) because the flowers of the central genera of Mariceae, *Neomarica* and *Trimezia*, have exactly the same structure. The genera of Mariceae, however, have a rhizomatous rootstock and plane leaves, and these features are less specialized than the bulb and plicate leaves of Tigridieae. In the other New World tribe of Iridoideae, Sisyrinchieae, which also has a rhizomatous rootstock and plane leaves, the inner and outer tepals are similar, not normally unguiculate, lack a zone of nectaries, and have style branches that are always simple, filiform structures sometimes reduced to short lobes.

Thus, the pattern of floral evolution in Tigridieae, as presented in the cladogram (Fig. 3), is best seen as a progressive reduction from the complex to the simple (Figs. 1, 2). Goldblatt (1990) presented this argument in detail. To consider the phylogenetic relationships as having a different pattern, from the simple to the complex, is tempting. It is, however, less parsimonious as this means that either the exact type of flower structure evolved independently in Mariceae and Tigridieae, or that Mariceae are derived from supposedly specialized

FIGURE 2. Flowers, style, and stamen detail and enlargement of style branch apex in selected Iridaceae.—A. *Trimezia steyermarkii*.—B. *Onira unguiculata*.—C. *Gelasine elongata* (= *G. azurea*).—D. *Eleutherine bulbosa*. Habit and flowers full size; stamens and style × 3; style branch apices much enlarged.

Tigridieae and acquired a rhizome and plane leaves secondarily. Both scenarios seem unlikely. In Irideae, a similar progression from the complex type of flower to the simple seems likely (Goldblatt, 1981, 1986, 1990) and the same pattern seems to have occurred in *Cipura*, a small genus of Tigridieae (Goldblatt & Henrich, 1987).

In the scenario outlined above, *Calydorea* appears to be a moderately specialized member of Tigridieae. It most likely evolved from a *Cypella*-like ancestor in which the style branches lost their thickening and apical appendages, and differences between the inner and outer tepals were reduced (Fig. 3). The flower of *Catila amabilis* is interpreted here as being close to this ancestral type, and *Calydorea pallens* represents another step in this process, leading to species with flowers like *C. speciosa*, and ultimately to such Northern Hemisphere species as *C. coelestina* and *C. longispatha*, with their secund flowers and elongate, eccentric style (Fig. 3).

Other genera of Tigridieae with simple style branches resembling those of *Calydorea* are *Eleutherine* Herbert (1843b), which comprises two species; one species of *Gelasine* Herbert (1840), *G. elongata* (= *G. azurea*); and *Onira* Ravenna (1983). Regarding *Eleutherine* (Fig. 2D), we feel that it is unrelated to *Calydorea*. Its unusual reddish bulb, large subterminal cauline leaf, and short inflorescence spathes seem to isolate it from possible relatives. The reduction of this genus should be considered when its immediate ancestry can be

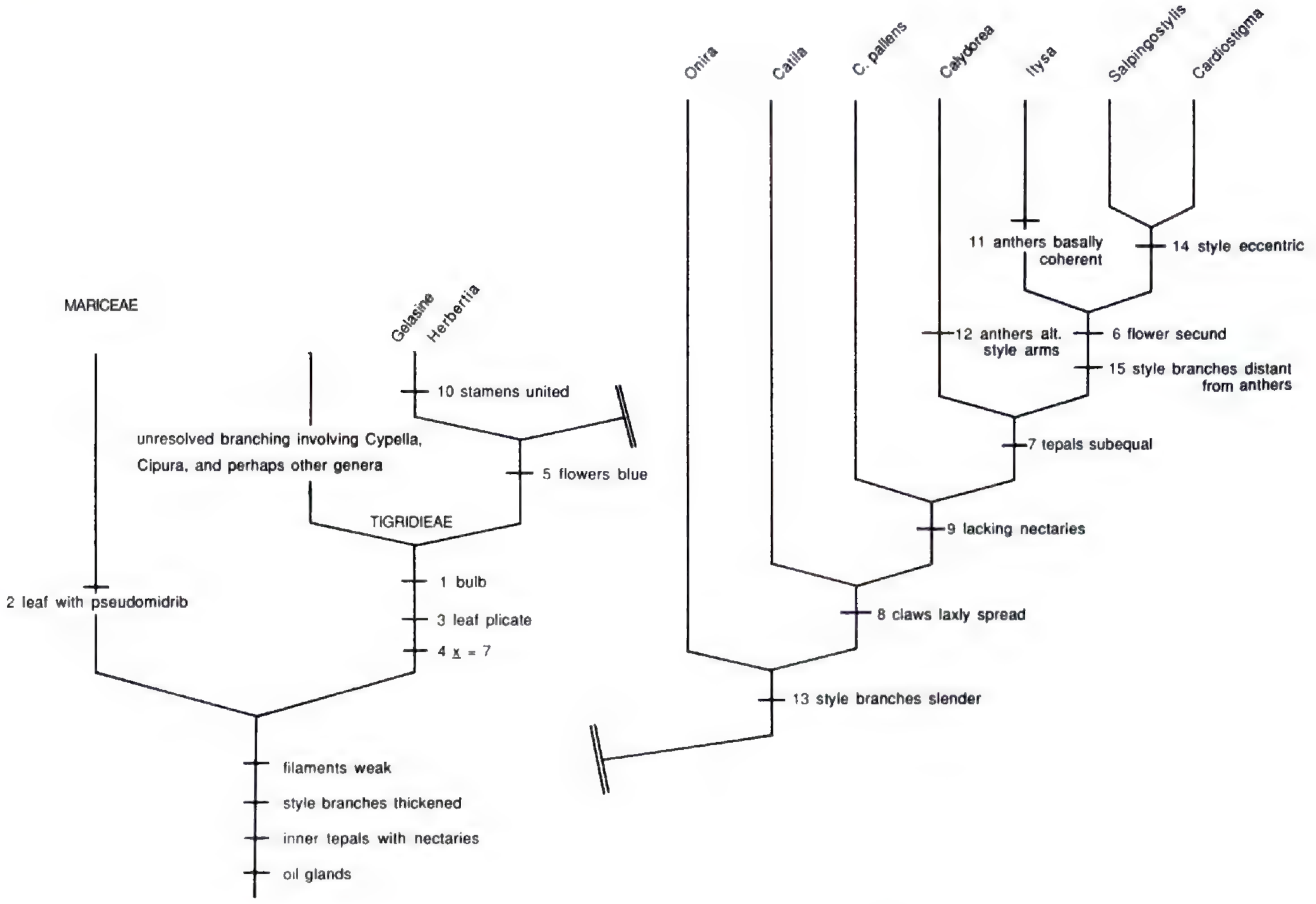

FIGURE 3. Phylogeny of the genera and species closely allied to *Calydorea* suggested by the cladogram based on the character list and data matrix presented in Table 1. The major branching patterns in Tigridieae and sister tribe Mariceae (from Goldblatt, 1990) are indicated to give some perspective to the *Onira–Calydorea* clade. Polarity of unnumbered characters from Goldblatt (1990).

TABLE 1. Data matrix and character list for the cladogram (Fig. 3). Presence of the specialized condition is denoted by 1; absence by 0; state inapplicable by ?

Genus	Character number														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mariceae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Calydorea	1	0	1	1	1	0	1	?	1	0	0	1	1	0	0
C. pallens	1	0	1	1	1	0	0	1	1	0	0	0	1	0	0
Salpingostylis	1	0	1	1	1	1	1	?	1	0	0	0	1	1	1
Cardiostigma	1	0	1	1	1	1	1	?	1	0	0	0	1	1	1
Itysa	1	0	1	1	1	1	1	?	1	0	1	0	1	0	1
Catila	1	0	1	1	1	0	0	1	0	0	0	0	1	0	0
Onira	1	0	1	1	1	0	0	0	0	0	0	0	1	0	0
Cypella	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
other genera, e.g.,															
Gelasine, Herbertia	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0

Characters: the derived (apomorphic) states listed first followed by the presumed ancestral (plesiomorphic) condition.

1. rootstock a bulb—rootstock a rhizome; 2. leaf with pseudomidrib—leaf without pseudomidrib; 3. leaf plicate—leaf plane; 4. basic chromosome number $x = 7$—base number not $x = 7$ (but unknown); 5. flowers shades of blue—flowers shades of yellow; 6. flower secund—flower upright; 7. tepals subequal and not clawed—tepals unequal and clawed; 8. tepal claws laxly spread—claws forming an open cup; 9. tepals lacking nectaries—zone of nectaries present on inner tepals; 10. stamens united—stamens free; 11. anthers coherent at base—anthers separate from one another; 12. anthers alternating with the style branches—anthers opposite the style arms; 13. style branches slender and not forked—style arms thickened and apically forked; 14. style eccentric—style central; 15. style branches distant from the anthers—style branches at same level as anthers.

identified. The subterminal cauline leaf, rather fleshy bulb scales, and basic chromosome number, $x = 6$, suggest that it is possibly a derivative of *Gelasine*. Base number in Tigridieae is $x = 7$ (Goldblatt, 1982), and apart from *Eleutherine*, $x = 6$ is known in the tribe only in *G. elongata* (reported as *G. azurea*) (Kenton & Rudall, 1987). The similarity in the karyotypes in these two is striking and may indicate a relationship.

Gelasine elongata (Fig. 2C) has united filaments and is a large plant, resembling *G. coerulea* and *G. uruguaiensis* vegetatively. These two species also have united filaments but more elaborate style branches that have paired crests and a broad transverse, abaxial stigma (Ravenna, 1984). *Gelasine elongata* is an autogamous, complex heterozygote (Kenton & Rudall, 1987) with a reduced basic chromosome number, $n = 6$, unlike most Tigridieae, which have $x = 7$. It seems likely that the apparently simple flower and style of *G. elongata* are the result of reduction from the more complex structures present in other species of *Gelasine*. Chromosome number is known in only one other *Gelasine*, *G. uruguaiensis*, $n = 7$ (Ravenna, 1984). Presumably, *Gelasine* evolved from a *Cypella*-like ancestor, and the major distinction between the two genera is in the filaments, free and long in *Cypella*, short and united in *Gelasine*. We assume that similar patterns of floral evolution occurred in *Gelasine* and *Calydorea*. In both genera species have evolved with flowers with subequal unclawed tepals and simple cylindric style branches lacking crests.

Onira

Described in 1983 by Ravenna, *Onira* includes only *O. unguiculata* (Baker) Ravenna, based on *Herbertia unguiculata*. It is a small plant with large, pale blue-green flowers (Fig. 2B). Apart from the color and size of the tepals, and the well-developed tepal claws, the flower is unusual only in the short style, which divides below the middle of the filaments, and the comparatively long, slender style branches (Fig. 2B detail). The filaments are free and the anthers are appressed to the style branches and are closely held to them by the recurving of the anther sacs after anthesis. The style branch apices resemble fairly closely those of *Calydorea pallens* and *Catila* except for the small, irregular outgrowths of nonstigmatic tissue on the stigma lobes (Fig. 2B detail). These may represent the vestigial remains of the style crests that are so prominent in, for example, *Cypella*, and hypothesized as plesiomorphic for the tribe. The tepal whorls are well differentiated, the inner being much smaller than the outer, and strongly folded back at the juncture of the limb and claw. This differentiation is much more pronounced than in *Catila*. We feel that *Onira* and related genera should be studied further before a decision is made regarding their status and disposition.

Systematic Treatment

Calydorea Herbert, Bot. Reg. 29, Misc. Matter.: 85. 1843. TYPE: *C. speciosa* (Hook.) Herbert (= *C. xiphioides* (Poeppig) Espin.).

Cardiostigma Baker, J. Bot. London 14: 188. 1876. TYPE: *C. longispathum* (Herbert) Baker (= *Calydorea longispathum* (Herbert) Baker).

Salpingostylis Small, J. New York Bot. Gard. 32: 161. 1931. TYPE: *S. coelestinum* (Bartr.) Small (= *Calydorea coelestina* (Bartr.) Goldbl.).

Catila Ravenna, Nordic J. Bot. 1983. TYPE: *C. amabilis* Ravenna (= *C. amabilis* Ravenna) Goldbl.

Itysa Ravenna, Nord. J. Bot. 6: 582. 1986. TYPE: *I. gardneri* (Baker) Ravenna (= *Calydorea gardneri* Baker).

Nomenclature of species of *Calydorea* discussed in this paper, including new combinations

1. **Calydorea coelestina** (Bartr.) Goldbl. & Henrich, comb. nov. BASIONYM: *Ixia coelestina* Bartr., Trav. ed. 1, Philadelphia, 155 (1791) [ed. 1, London, 153 & pl. 3 (1792)]; *Salpingostylis coelestina* (Bartr.) Small, J. New York Bot. Gard. 32: 161 (1931). [See Goldblatt (1974) for additional homotypic synonyms.] TYPE: Illustration in Bartram, Travels, pl. 3.
2. **Calydorea longispatha** (Herbert) Baker, J. Bot. London 14: 189 (1876). BASIONYM: *Gelasine longispatha* Herbert in Benth., Pl. Hartweg. 53 (1840). *Cardiostigma longispatha* (Herbert) Baker, J. Linn. Soc. Bot. 16: 102 (1878); *Sphenostigma longispathum* (Herbert) Benth. & Hook., Gen. Pl. 3(2): 695 (1883). TYPE: Mexico. *Hartweg 403* (BM, G) [See Foster (1945: 12) for additional homotypic synonyms.]
3. **Calydorea mexicana** (R. Foster) Goldbl. & Henrich, comb. nov. BASIONYM: *Sphenostigma mexicanum* R. Foster, Contr. Gray Herb. 155: 13 (1945); *Cardiostigma mexicana* (R. Foster) Ravenna, Notic. Mens. etc. (1978). [Additional homotypic synonyms in Foster (1945).] TYPE: Mexico. México: Temascaltepec, Carboneras, *Hinton et al. 8010* (holotype, GH; isotypes, F, MO, NY, US).

4. **Calydorea gardneri** Baker, J. Bot. London 14: 188. 1876. *Itysa gardneri* (Baker) Ravenna, Nord. J. Bot. 6: 582. 1986. TYPE: Brazil. Piauí: Bôa Esperanca, *Gardner 2322* (holotype, BM not seen). [Known to us from illustrations in Ravenna (1986).]
5. **Calydorea venezolensis** (Ravenna) Goldbl. & Henrich, comb. nov. BASIONYM: *Itysa venezolensis* Ravenna, Nord. J. Bot. 6: 584. 1986. TYPE: Venezuela. Guárico: *Ravenna 2178* (holotype, Herb. Ravenna not seen). [Known to us only from the illustrations in the protologue.]
6. **Calydorea amabilis** (Ravenna) Goldbl. & Henrich, comb. nov. BASIONYM: *Catilla amabilis* Ravenna, Nord. J. Bot. 3: 197. 1983. TYPE: Argentina, Entre-Rios, *Ravenna 3* (holotype, Herb. Ravenna not seen). [Known to us from the illustrations in the protologue and from living material.]

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CHROMOSOME NUMBERS IN THE GENUS *NASSAUVIA* (COMPOSITAE–MUTISIEAE)[1]

J. H. Hunziker,[2,3] *A. F. Wulff,*[3] *T. F. Stuessy,*[4] *D. J. Crawford,*[4] *and J. V. Crisci*[5]

Abstract

Meiotic chromosome numbers were determined (n = 11 and ca. 44; x = 11) and observations made for eight species of *Nassauvia* (Compositae, Mutisieae). The numbers include counts for seven species that have not previously been investigated cytologically: *N. axillaris*, *N. chubutensis*, *N. glomerulosa*, *N. lagascae*, *N. revoluta*, and *N. uniflora* (all with n = 11) and *N. aculeata* (with n = ca. 44). The results reveal three known chromosomal levels for the genus: n = 11 ($2x$), n = 22 ($4x$), and n = ca. 44 ($8x$). Infraspecific polyploidy in *Nassauvia* is known in *N. magellanica* with both n = 11 and 22. The closest generic relatives are *Calopappus* and *Triptilion*, but no cytological data are yet available for them. The most closely related genus for which chromosomal data are available is *Moscharia* with n = 20, which suggests that it and *Nassauvia* could be based on x = 11 (or perhaps x = 10).

The genus *Nassauvia* Comm. ex A. L. Juss. of the Compositae belongs to the tribe Mutisieae, subtribe Nassauviinae. It comprises 38 species (Cabrera, 1982; Arroyo & Marticorena, 1988) distributed from southern Bolivia along the Andes to southern Patagonia, Tierra del Fuego, and the Malvinas (Falkland) Islands. The genus demonstrates a trend toward reduction of numbers of flowers in each capitulum and aggregation of capitula into secondary inflorescences, or pseudocephalia.

The cytology of this genus has been poorly studied. Chromosome numbers are known only from four (10%) of the species. The following numbers have already been documented: n = 11 for *N. darwinii*, *N. magellanica*, and *N. serpens*; and n = 22 for *N. gaudichaudii* and *N. magellanica* (Moore, 1967, 1981; Crisci, 1974b; Cabrera, 1982). The present study presents chromosomal data for additional species of the genus and comments on their systematic and evolutionary significance.

Materials and Methods

Meiotic investigations were made from young inflorescences fixed in modified Carnoy's solution (4 : 3 : 1, chloroform : ethanol : acetic acid) or modified Newcomer's solution (Hunziker, 1966). The latter proved superior. Root tips were squashed in 45% propionic acid haematoxylin (2%) with ferric citrate (1%) used as mordant (Saez, 1960; Nuñez, 1968). Preparations were mounted in Euparal after removal of the coverslip by freezing with carbon dioxide. Voucher specimens are deposited at LP. The sources of the materials collected in Argentina are presented in Table 1.

Results and Discussion

In the diploid species (*N. axillaris*, *N. chubutensis*, *N. darwinii*, *N. glomerulosa*, *N. lagascae*, *N. revoluta*, and *N. uniflora*) meiosis was regular with $2n$ = 11II (Fig. 1A, C–H). In contrast, *N. aculeata* (Fig. 1B) was found to be octoploid with $2n$ = ca. 44 bivalents. Except for *N. darwinii*, all of these species are reported here for the first time. With these new counts, 11 species (29%) of *Nassauvia*, including species from each section, have been analyzed cytologically. The basic number is clearly x = 11, with three ploidy levels: $2x$, $4x$, and $8x$. This basic number is also known in other genera of the Nassauviinae, e.g., *Holocheilus* Cass.

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TABLE 1. New chromosome counts of species of *Nassauvia*. Vouchers on deposit at LP, OS, and SI.

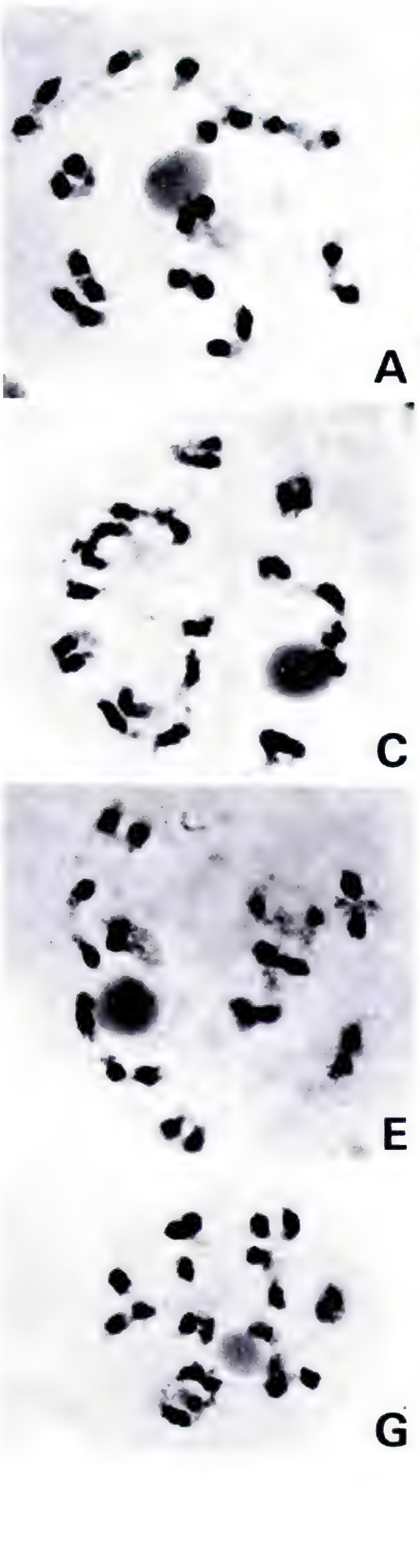
Taxon	Chromosome count	Number of cells studied	Location and voucher[1]
N. aculeata (Less.) Poeppig var. *robusta* (Cabrera) Cabrera	n = ca. 44	3	Prov. Chubut, Dep. Futaleufú, 45 km SE de Esquel, sobre ruta 40, hacia Tecka, 4 Dec. 1984, *TFS, DJC, JVC, MMC & MG 6842*
N. axillaris (Lagasca) D. Don	n = 11	3	Prov. Chubut, Dep. Languiñeo, 37 km al E de Tecka, ruta prov. 63 hacia Quichaura, 6 Dec. 1984, *TFS, DJC, JVC, MMC & MG 6868*
N. chubutensis Speg.	n = 11	6	Prov. Chubut, Dep. Mártires, 9 km al S de Las Chapas (ruta 31), 8 Dec. 1984, *TFS, DJC, JVC, MMC & MG 6946*
N. darwinii (J. D. Hook. & Arn.) O. Hoffm. & Dusén	n = 11	24	Prov. Chubut, Dep. Languiñeo, ca. 6.5 km E de Lago Vinter, 7 Dec. 1984, *TFS, DJC, JVC, MMC & MG 6894*
N. glomerulosa (Lagasca) D. Don	n = 11	18	Prov. Chubut, Dep. Languiñeo, 10 km E de Tecka, ruta hacia Quichaura, 6 Dec. 1984, *TRS, DJC, JVC, MMC & MG 6863*
N. lagascae (D. Don) F. Meigen	n = 11	12	Prov. Mendoza, Dep. San Carlos, Borde SW de Laguna Diamante, 3,370 m, 27 Jan. 1985, *JHH, AFW & NGG 11326*
N. revoluta D. Don	n = 11	7	Prov. Chubut, Dep. Futaleufú, Cerro La Hoya, 15 km NE de Esquel, 5 Dec. 1984, *TFS, DJC, JVC, MMC & MG 6857*
N. uniflora (D. Don) Hauman	n = 11	15	Prov. Mendoza, Dep. Las Heras, alrededores Laguna Los Horcones, 3,180 m, 16 Jan. 1985, *JHH, AFW & NGG 11163*
N. uniflora (D. Don) Hauman	n = 11	24	Prov. Mendoza, Dep. Las Heras, Laguna Los Horcones, 3,050 m, 17 Jan. 1985, *JHH, AFW & NGG 11183* [Fig. 1A]
N. uniflora (D. Don) Hauman	n = 11	4	Prov. Mendoza, Dep. Las Heras, Playa Ancha, Quebrada del Tolosa, 3,660 m, 18 Jan. 1985, *JHH, AFW & NGG 11195*
N. uniflora (D. Don) Hauman	n = 11	2	Prov. Mendoza, Dep. Luján, Las Cuevas, 3,160 m, 19 Jan. 1985, *JHH, AFW & NGG 11205*

[1] JHH, AFW, and NGG = J. H. Hunziker, A. F. Wulff, and N. G. Galiano; TFS, DJC, JVC, MMC, and MG = T. F. Stuessy, D. J. Crawford, J. V. Crisci, M. M. Cigliano, and M. Gentile.

(n = 11; Coleman, 1968; also reported with n = 18, Crisci, 1976) and *Marticorenia* Crisci (n = 22; Crisci, 1974a). However, these two genera are not included in the same evolutionary cluster in the phylogenetic reconstructions of the subtribe by Crisci (1974b, 1980).

Although most of the species of *Nassauvia* are diploids, three polyploids are known. *Nassauvia aculeata* is n = ca. 44 (octoploid). The other counted species of sect. *Panargyrum* are diploid (n = 11; *N. darwinii* and *N. uniflora*). The chromosomes of *N. aculeata* are smaller than those of the diploids, a relationship also observed in other groups (Darlington, 1963; Grant, 1976). This could be due to (1) smaller chromosome size in diploid progenitors, or (2) chromosome size reduction after the ploidy jump occurred (e.g., Poggio & Hunziker, 1986). Of all the species of *Nassauvia*, *N. aculeata* is particularly variable morphologically and has a wide geographic distribution. Taxonomically this has resulted in the recognition of three varieties (Cabrera, 1982). The wide range of *N. aculeata* may be due at least in part to its polyploid condition and genetic diversity. More populational sampling is needed to determine if infraspecific chromosomal races are present, such as documented in *N. magellanica* J. Gmelin (see below) and as known in other members of the family (e.g., in *Melampodium* L.; Stuessy, 1971).

The second polyploid in *Nassauvia* is *N. gaudichaudii*, a tetraploid with n = 22. The five other species of this section, *N. ameghinoi* Speg., *N.*


A

B

C

D

E

F

G

H

hillii, *N. juniperina* Skottsb., *N. pentacaenoides*, and *N. pygmaea* (Cass.) J. D. Hook, are unknown chromosomally. Material of *N. hillii* and *N. juniperina* was attempted without success.

The third case of polyploidy in *Nassauvia* is *N. magellanica* in which both $n = 11$ (Moore in Crisci, 1974b) and $n = 22$ (Moore, 1981) have been recorded. This infraspecific polyploidy occurs in a taxon of the relatively advanced sect. *Nassauvia*, which contains species with high degrees of head condensation.

Within the subtribe Nassauviinae, *Nassauvia* is closest both phenetically and cladistically to *Triptilion* Ruíz Lopez & Pavón and *Calopappus* Meyen (Crisci, 1974b, 1980; Crisci & Freire, 1986). As chromosome counts are not yet available for these two genera, however, the generic relationships cannot be assessed cytologically. The next closest relatives of *Nassauvia* are probably *Polyachyrus* Lagasca and *Moscharia* Ruíz Lopez & Pavón (Crisci, 1974b, 1980), and the latter has $n = 20$ (Crisci, 1974b). This suggests a base number of $x = 10$ or 11 for the ancestral stock of these genera and that *Moscharia* is probably polyploid. Other more distant relatives might include *Panphalea* ($n = 8$), *Holocheilus* ($n = 11$ and 18), and *Perezia* ($n = 4, 8, 12$), but the relationships of these genera are uncertain and differ depending upon the phenetic or cladistic algorithm used. Other recorded chromosome numbers in the subtribe (summarized in Crisci, 1974b) are $n = 27$ in *Acourtia* D. Don, $n = 18$ in *Jungia* L. f., $n = 22$ for *Marticorenia*, and $n = 27$ for *Proustia* Lagasca and *Trixis* P. Browne.

For insights on evolution within *Nassauvia*, the most likely outgroup of *Nassauvia* seems to be *Calopappus*, which possesses large single capitula (Crisci & Freire, 1986). The other closely related genus, *Triptilion*, seems best regarded as having evolved from *Nassauvia*. *Triptilion* has different aggregations of heads, but most are moderately clustered in the axils of the leaves. We regard this as perhaps having come from sect. *Panargyrum* of *Nassauvia*, which has similar levels of intermediate head aggregation. The most primitive section of *Nassauvia* is probably *Mastigophora*, particularly *N. pentacaenoides* Speg., which resembles *Calopappus* in head aggregation, leaf arrangement, and rhizomatous habit.

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Figure 1. Meiotic chromosomes of species of *Nassauvia*.—A. *N. uniflora*.—B. *N. aculeata*.—C. *N. revoluta*.—D. *N. axillaris*.—E. *N. darwinii*.—F. *N. chubutensis*.—G. *N. lagascae*.—H. *N. glomerulosa*. All same scale. A–G = diakinesis, H. = prometaphase I.

DASYLIRION WHEELERI VAR. *DURANGENSE*: A NEW COMBINATION IN THE NOLINACEAE[1]

Joseph E. Laferrière[2]

Abstract

Fruits from 34 specimens of a single population of *Dasylirion* from the Sierra Madre Occidental of Chihuahua, Mexico, were compared with those of herbarium specimens of *D. wheeleri* and *D. durangense* from outside the study area. Variation was found in this population spanning the range between the two taxa. It was concluded that *D. wheeleri* and *D. durangense* are conspecific, and the latter is reduced to varietal status. *Dasylirion wheeleri* var. *durangense* is also reported for the first time from Sonora.

The genus *Dasylirion* Zucc. is a member of the Nolinaceae with approximately 15 species native to Mexico and the southwestern United States. The plants are large, perennial, rosette herbs with strap-like leaves and flowering stalks up to 6 m tall. Various authors have merged this family with the Liliaceae or the Agavaceae (Cronquist, 1981), but more recent workers have supported separating the group as a distinct family (Dahlgren et al., 1985).

Trelease (1911) described several new species and varieties of *Dasylirion* based largely on differences in the morphology of the three-winged, one-seeded samara. In particular, *D. durangense* Trel., a species described from a single specimen collected from Durango, Mexico, was said to have fruits "broadly elliptical-cordate, 7–8 × 9 mm," and the style "scarcely half as long as the rather open deep notch." This was contrasted with the more widespread *D. wheeleri* S. Wats. in Rothr., which was characterized by fruits "round-obovate, 6–7 × 7–9 mm, the style normally about equalling the open moderately deep notch." To date, only two publications have compared these two species, both of which have relied almost exclusively on Trelease's descriptions (Standley, 1920; Conzatti, 1947). The present analysis of a population in which both taxa occur sympatrically was conducted to ascertain the utility of the length of the style and the shape of the capsule wings in distinguishing *D. wheeleri* from *D. durangense* and to determine whether the distinction between the two taxa should continue to be recognized at the species level.

Materials and Methods

The site chosen for study on sympatric populations was the village of Nabogame, Chihuahua, Mexico. The town lies at 28°30′N, 108°30′W, approximately 1,800 m in the Sierra Madre Occidental, approximately 10 km east of the frontier with the state of Sonora. This site is ideal for such a study since plants referable to both *D. wheeleri* and *D. durangense* may be found growing within a few meters of one another. This is the most northerly location from which *D. durangense* has been reported in the literature (Fig. 1).

Fruits were collected from 34 individuals within 2 km of Nabogame. This sample represented the maximum number of individuals that could be collected within a two-week period. Most of the plants were located on extremely steep granitic slopes subject to less disturbance than other habitats in the area. Since the shape of the wings changes as the capsule matures, fruits were collected in December 1987, after they had fully dried. From each individual, ten fruits were selected for measurement on the basis of absence of insect damage and teratological deformities, and the presence of an unbroken style. Measurements were made as shown in Figure 2.

For comparison, herbarium specimens of *D.*

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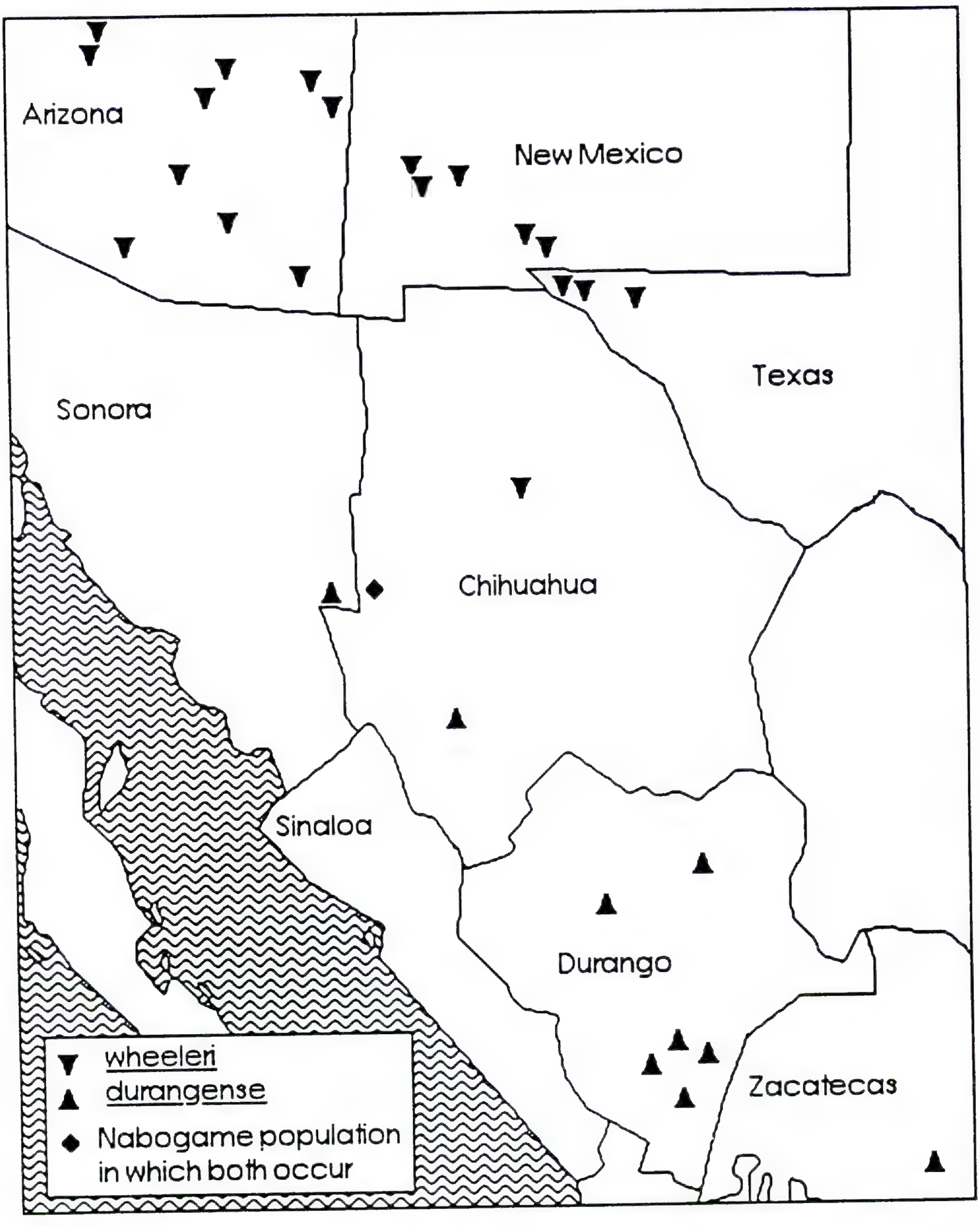

FIGURE 1. Map showing Nabogame and the distribution of *Dasylirion wheeleri* and *D. durangense*. Diamond represents Nabogame population, where both taxa are present.

wheeleri and *D. durangense* from outside the Nabogame area were also measured. Fourteen specimens of *D. wheeleri* and six of *D. durangense* with mature fruits were examined, including both the type specimen of *D. durangense* and the one syntype of *D. wheeleri* with mature fruits. The same measurements were made on these specimens as on the fruits collected from Nabogame.

In addition, leaf and flower characters were examined on a much larger number of specimens, but no consistent differences between the two taxa were noted. In particular, the size of the teeth and of the denticules between them, characters used by Trelease in his taxonomic discussions, varied widely in northern and in southern collections.

RESULTS

Averages and standard deviations of the three samples are given in Table 1. An analysis of vari-

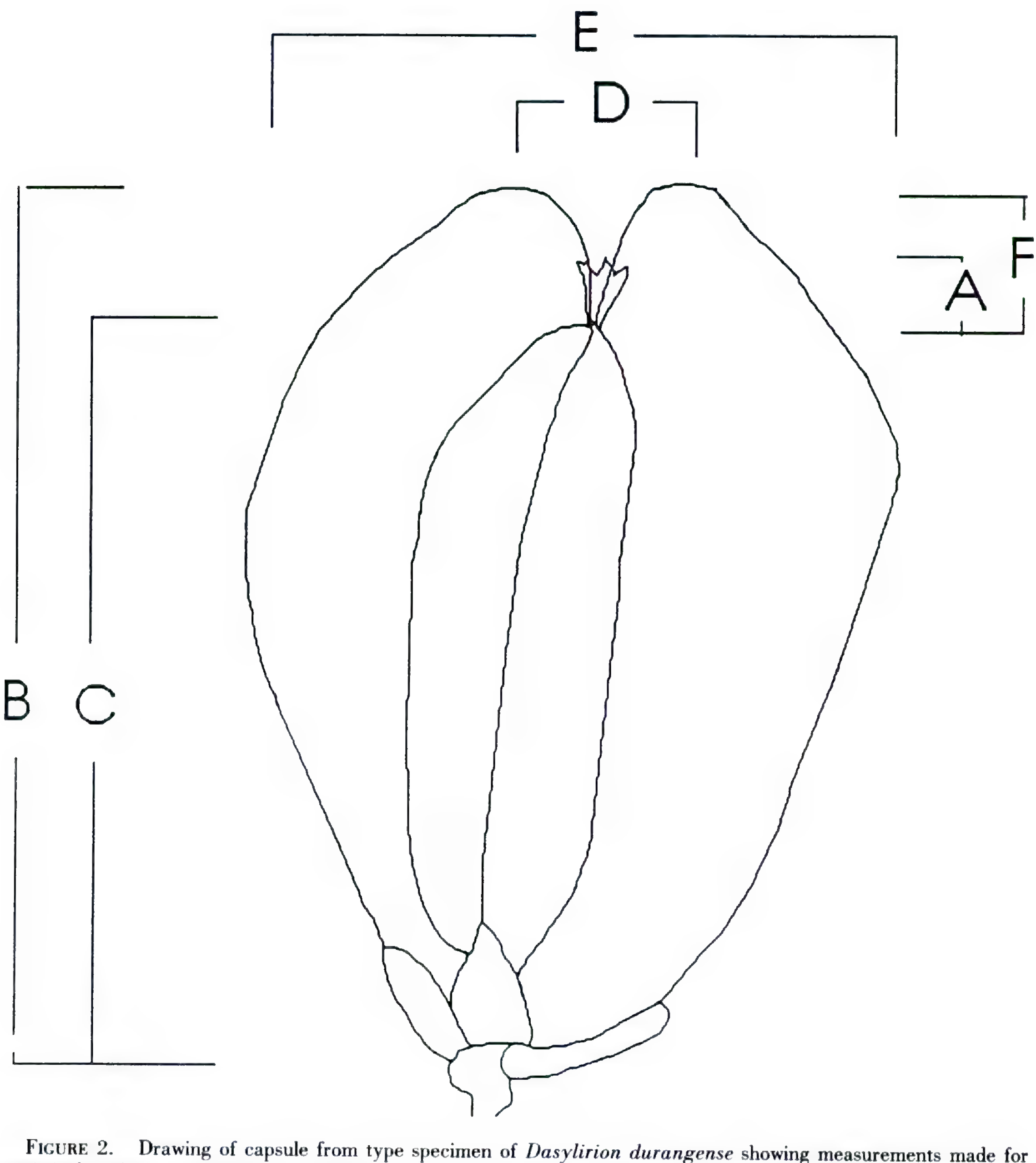

FIGURE 2. Drawing of capsule from type specimen of *Dasylirion durangense* showing measurements made for statistical analysis. A represents the length of the style, B the length of the entire fruit, C the length of the main axis from the base of the fruit to the base of the style, D the width of the notch, i.e., the distance between the wings at their point of maximum distance from the base of the fruit, and E the maximum width of the fruit. From these measurements were calculated F, the notch depth, i.e., the height of the wings above the base of the style (B − C), and G, the ratio of the length of the style to the depth of the notch (A/F).

ance (ANOVA) test was performed on each of the seven characters; highly significant differences were found between the three samples at the 1% level for all seven characters. The data were subjected to a Newman-Keuls' specific comparison test to ascertain where the differences lie (Linton & Gallo, 1975); a Student's *t*-test yielded results identical to those produced by the Newman-Keuls' test. Results are indicated in Table 1.

The data gathered from herbarium specimens showed statistically highly significant differences between the two taxa in three of the eight characters measured: total length, notch depth, and style/notch ratio. In addition, there was a signifi-

TABLE 1. Means and standard deviations of *Dasylirion* fruit measurements. Data for *D. wheeleri* and *D. durangense* represent herbarium specimens collected outside the Nabogame area.

	D. wheeleri	*D. durangense*	Nabogame population
N	14	6	34
A (style length, mm)	0.80 ± 0.09	0.90 ± 0.10	0.95 ± 0.11**
B (total length, mm)	6.48 ± 0.78§§	8.36 ± 0.78**	8.29 ± 0.89**
C (axis length, mm)	5.54 ± 0.63	6.12 ± 0.79	6.25 ± 0.70**
D (notch width, mm)	2.39 ± 0.76	2.41 ± 0.44	3.94 ± 0.74**§§
E (total width, mm)	5.02 ± 0.95§	5.97 ± 0.66*	6.77 ± 0.79**§
F (notch depth, mm)	1.21 ± 0.38§§	2.24 ± 0.62**	2.04 ± 0.51**
G (style/notch ratio)	0.70 ± 0.17§§	0.26 ± 0.11**	0.53 ± 0.17**§§

*—Significantly different from *D. wheeleri* (5% level) using a Newman-Keuls' or a *t*-test.
**—Highly significantly different from *D. wheeleri* (1% level).
§—Significantly different from *D. durangense* (5% level).
§§—Highly significantly different from *D. durangense* (1% level).

cant difference in total width at the 5% level. The Nabogame data differ statistically from the *D. wheeleri* sample in all characters measured, even those for which the latter did not differ from *D. durangense*. Notch width and style/notch ratio showed highly significant differences between Nabogame and *D. durangense*, while total width showed a difference significant at the 5% level. Despite these statistical differences, for each character individuals in the Nabogame population exist which exhibit the characteristics of each of the two recognized taxa. Indeed, in every case the variation in the Nabogame population exceeds the entire range between the mean values for the two taxa.

In addition to the characters included in the statistical analyses, there is considerable variation in general wing shape, a character less readily quantifiable than those chosen for measurement. Similar variation is also apparent among the herbarium specimens. Most of this is between individuals, but some is between different fruits from the same plant.

DISCUSSION

The length of the style in fruit is useless as a diagnostic character. The shape of the wings may have some taxonomic value, but there is a great deal of phenotypic variation even within a single population. It thus appears that *D. wheeleri* and *D. durangense* should not be maintained as separate species.

It does seem desirable, however, to recognize *D. durangense* as a variety of *D. wheeleri*, in view of the consistent difference in notch depth between specimens from the southern part of the range and those from further north. Yet there is considerable variation and intergradation between the two taxa. It is not known whether there exists a north-south cline connecting the two extremes or a narrow zone of intermediates in the area around Nabogame. In terms of notch depth, the Nabogame population appears more closely related to var. *durangense*, but it spans the range between the two extremes. Even in terms of notch width, the one character statistically separating the population from both of the recognized taxa, the variation is so great that if this one trait was used as a diagnostic character to describe a third variety, different individuals in the Nabogame population would be assignable to each of the three taxa. The notch-depth character singled out by Trelease is only part of a much broader variability than implied by his recognition of *D. durangense* as a distinct species.

TAXONOMY

In view of the preceeding, the following change is indicated:

Dasylirion wheeleri S. Wats. in. Rothr. var. **durangense** (Trel.) Laferrière, comb. et stat. nov. *Dasylirion durangense* Trel., Proc. Amer. Philos. Soc. 50: 438. 1911. TYPE: *Palmer 557*.

The name "wheeleri" has precedence because it was first published in 1878 (Rothrock, 1878). The present paper is the first to report *D. wheeleri* var. *durangense* from Sonora (Gentry, 1972). The two varieties may be distinguished by the following key:

1a. Distal wing tips in fruit extending more than 1.5 mm above base of style ..... var. *durangense*
1b. Distal wing tips extending less than 1.5 mm above base of style ..... var. *wheeleri*

Selected specimens examined. **Dasylirion wheeleri** var. **wheeleri.** MEXICO. CHIHUAHUA: Nabogame, 28°30′N, 108°30′W, 6 Dec. 1987, *Laferrière 1314* (ARIZ, MEXU, MO). SONORA: Río Bavispe, 30°20′N, 109°W, 11 Aug. 1940, *White 3234* (LL). UNITED STATES. ARIZONA: Cochise Co., 11 Nov. 1967, *Barr 67-437* (ARIZ); 2 Jan. 1983, *Yatskievych & Windham 83-03* (ARIZ); Gila Co., 16 Sep. 1973, *Engard 105* (ARIZ); Pinal Mts., Gila Co., 30 July 1892, *Toumey 449* (MO); Graham Co., Ash Creek, 1874, *Rothrock 655* (syntype) (MO); Greenlee Co., 7 Oct. 1942, *Wolf & Everett 11404* (ARIZ); Pima Co., 8 km E of Vail, 7 Sep. 1938, *Crooks, Thornber & Benson s.n.* (ARIZ); Pinal Co., Oracle, 9–13 Sep. 1905, *Thornber s.n.* (ARIZ); Mazatzal Mts., Tonto National Forest, 5 Nov. 1975, *Gentry & Gentry 23618* (ARIZ). NEW MEXICO: Grant Co., near Silver City, Aug.–Sep. 1911, *Holzinger s.n.* (MO); TEXAS: El Paso 12 km N of El Paso, 29 Sep. 1956, *Warnock 14255* (LL).

Dasylirion wheeleri var. **durangense.** MEXICO. CHIHUAHUA: Nabogame, 28°30′N, 108°30′W, 15 Nov. 1988, *Laferrière 2268* (ANSM, ARIZ, MEXU, MO); Quirire, Mpio. Batopilas, 3 June 1984, *Bye, Davis, Randolph & Gerson 12854* (COLO). DURANGO: Durango City, *Palmer 557* (type) (MO, MEXU); km 249 on Highway 45 between Durango and Zacatecas, 24 July 1985, *Starr 903* (ARIZ); 9 km W of Cd. Durango on Highway 40, 6 Aug. 1975, *Gentry & Engard 23613* (ARIZ); 24 km E of La Zarca, on Highwy 30, 26 July 1958, *Correll & Johnston 20223* (LL); km 40 Durango-Mezquital Highway, 22 Apr. 1982, *Gonzalez s.n.* (LL); Durango, July 1911, *Ochoterena s.n.* (MO); SONORA: Maicoba, June 1968, *Pennington 91* (LL). ZACATECAS: Zacatecas, *Marroquin s.n.* (MEXU).

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NOTES

TWO NEW SPECIES OF *HILLIA* SUBG. *RAVNIA* (RUBIACEAE) FROM VENEZUELA AND MEXICO

Hillia Jacq. is a genus of about 24 species of succulent, usually epiphytic shrubs found throughout the moist and wet Neotropics. Subgenus *Ravnia* (Oersted) C. M. Taylor includes three species found in Costa Rica and Panama, plus the two species described below. The characteristics of this subgenus have been presented previously (Taylor, 1989). Recent collections have brought to scientific light the following two undescribed species, which are placed in subg. *Ravnia* based on the form and color of their corollas, which are tubular to narrowly funnelform, generally red in color, and presumably bird-pollinated.

Hillia rivalis C. M. Taylor, sp. nov. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, 3°43′N, 65°30′W, 1,200 m, 16 Oct. 1988 (fl, fr), *R. Liesner 24900* (holotype, MO; isotype, VEN). Figure 1.

Frutex subsucculentus, saxicola, glaber, ca. 1 m altus. Folia peranguste elliptica, 38–100 × 5–10 mm, apice basique acuta; petiolo 6–12 mm longo; stipulis 10–13 × 3–4 mm. Flores solitarii, 6-meri; pedunculo 1–2 mm longo; lobulis calycinis peranguste triangularibus, 18–36 × 1.5–2 mm; corolla infundibuliformi, externe sordide rubra, interne luteoviridi, tubo 32–59 mm longo, lobulis 8–10 × 6–10 mm; antheris ex parte exsertis. Capsula cylindrica, laevis, 50–65 × 8–10 mm, stipite 10–15 mm longo.

Glabrous, somewhat succulent, lithophytic shrubs to 1 m tall; bark smooth, red-brown to gray-brown. *Leaves* isophyllous; *blades* narrowly elliptic, 3.8–10 × 0.5–1 cm, narrowly acute at apex and base, coriaceous and hard upon drying, glabrous; secondary veins 4–5 pairs, obscure, pinnate, ascending, the distal 1–2 veins looping to interconnect, the midrib prominulous abaxially, the margins slightly involute; *petioles* 6–12 mm long, glabrous; *stipules* narrowly elliptic or lanceolate, 10–13 × 3–4 mm, acutely to broadly angled, membranaceous, glabrous, caducous. *Flowers* solitary, 6-merous; peduncles 1–2 mm long; bracts linear, 12 × ca. 0.5 mm, acute; ovary cylindrical, ca. 1 cm long, glabrous; *calyx* limb green, coriaceous, glabrous, divided nearly to base, tube 0–1 mm long, the lobes very narrowly triangular to linear, 18–36 mm long, 1.5–2 mm wide at base, acute; *corolla* funnelform, membranaceous, dull red externally, yellow-green internally, glabrous throughout, tube 3.2–5.9 cm long, 3–3.5 mm wide at base, the lobes triangular, 0.8–1 cm long, 6–10 mm wide at base, rounded to acutely angled, reflexed to revolute; *stamens* partially exserted, filaments 3–4 mm long, inserted ca. 4–6 mm below mouth of tube, anthers 8–9 mm long; *style* 3.4–6.5 cm long, stigma exserted, capitate, ca. 1–2 mm diam. *Capsules* cylindrical, woody to rather papery, brown, smooth, 5–6.5 cm long, 0.8–1 cm diam., borne on a stipe 1–1.5 cm long; *seeds* 1.5 × ca. 0.3–0.5 mm, with trichomes 1.2–1.5 cm long.

This new species was found growing on rocks in and along rivers, a habitat that has not been previously reported in *Hillia*, and which is emphasized in the specific epithet. One site was inundated a few days after the specimen was collected (R. Liesner, pers. comm.); presumably these perennial plants are adapted to such disturbance. In habit, leaf morphology, and capsule texture, *H. rivalis* strongly resembles the Mesoamerican shrub *Lindenia rivalis* Bentham, which grows in similar sites. These genera are apparently not closely related, and the resemblance is apparently one of convergence.

Hillia rivalis can be distinguished by its remarkably long, narrow calyx lobes, funnelform corollas that are red externally but yellow-green internally, relatively narrow leaves, and riverine habitat.

The floral morphology of this species strongly resembles that of several other species of *Hillia* with funnelform green corollas and pinnate leaf

FIGURE 1. *Hillia rivalis* (*Liesner 24900* MO), habit.

venation, notably *H. psammophila* Steyermark, *H. illustris* (Vellozo) K. Schumann, *H. foldatsii* Steyermark, and *H. saldanhaei* K. Schumann (Taylor, in prep.). The characteristics found in this species provide further evidence of a close relationship between the former genus *Ravnia* and *Hillia*.

This is the first report of a member of this subgenus from South America. The rather wide ranges of calyx lobe, corolla, and style dimensions

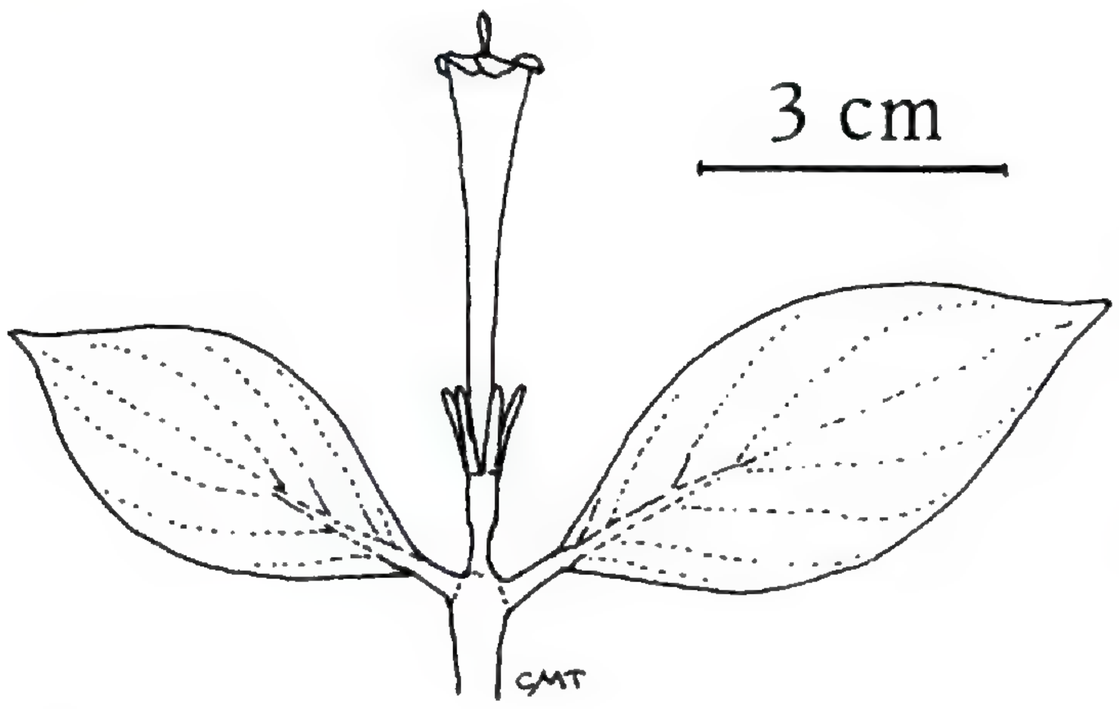

FIGURE 2. *Hillia oaxacana* (*Garcia M. & Torres C. 1523* MO), habit.

are derived from measurements of apparently mature structures all found in the same collection. Comparable variation is found in other species of *Hillia* (Taylor, in prep.).

Paratype. VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, Cerro Marahuaca, 3°38′N, 65°28′W, 1,225 m, 19 Feb. 1985 (fr), *R. Liesner 17712* (MO).

Hillia oaxacana C. M. Taylor, sp. nov. TYPE: Mexico. Oaxaca: distrito de Putla, Arroyo de San Isidro, 3 km al este de Concepción, Buenavista, 10 June 1985 (fl), *A. Garcia M. & R. Torres C. 1523* (holotype, MO; isotype, MEXU). Figure 2.

Frutex succulentus hemiepiphyticus, glaber. Folia elliptica, 4.2–6 × 2–2.5 cm, apice acuminata, basi cuneata; petiolo 5–8 mm longo. Flores solitarii, 6-meri; pedunculo 2–3 mm longo; lobulis calycinis lingulatis, ca. 6 × 1.5–2 mm; corolla tubiformi vel anguste infundibuliforme, tubo rubro ca. 3.8 cm longo, lobulis viridibus ca. 2.5 × 2.5 mm; antheris inclusis. Capsula ignota.

Glabrous, succulent, hemiepiphytic shrubs; bark smooth, gray. *Leaves* isophyllous; blades *elliptic*, 4.2–6 × 2–2.5 cm, acuminate at apex with the tip ca. 5 mm long, cuneate at base, subcoriaceous, glabrous; secondary veins 3–4 pairs, rather obscure, subpalmate, ascending, not looping to interconnect, not prominulous, margins straight; *petioles* 5–8 mm long, glabrous; *stipules* not seen. *Flowers* solitary, 6-merous; peduncles 2–3 mm long; bracts absent; ovary cylindrical, ca. 3 mm long, glabrous; *calyx* limb green, membranaceous, glabrous, divided to base, the lobes narrowly triangular, 6 mm long, 1.5–2 mm wide at base, rounded; *corolla* tubular to narrowly funnelform, carnose, red in tube, green on lobes, glabrous throughout, tube 3.8 cm long, 2 mm wide at base, the lobes triangular, 2.5 × 2.5 mm, broadly rounded, spreading to reflexed; *stamens* included, inserted above middle of tube, anthers 4 mm long, held 1–2 mm below mouth of tube; *style* 4 cm long, stigma exserted, with two clavate branches ca. 3 mm long. *Capsules* not known.

Hillia oaxacana can be distinguished by its tubular red corollas with green lobes and its leaves with the secondary veins all arising from below the middle of the blade ("subpalmate"). In its corollas, *H. oaxacana* is similar to *H. longifilamentosa* (Steyerm.) C. M. Taylor of Costa Rica and Panama, which differs in its completely red-orange corollas and long-exserted stamens. This new species is also similar to *H. saldanhaei* K. Schumann of Brazil, a poorly known species with similarly shaped but green corollas with lobes 6–7 mm long. Similar subpalmate leaf venation is found only in *H. ulei* K. Krause of Amazonian South America, which differs in its broadly funnelform green corollas. (*Hillia ulei* is here treated to include *H. viridiflora* Kuhlmann & Silveira, *H. irwinii* Steyermark, and *H. schultesii* Steyermark.) Reported here is the northernmost record of a member of subg. *Ravnia*. Specimens of the type collection were originally annotated and distributed as *H. macrocarpa* Standley & Steyermark, which *H. oaxacana* keys out to in the Rubiaceae treatment for the *Flora of Guatemala* (Standley & Williams, 1975).

I thank R. Liesner for field data, B. Manara for the illustration of *H. rivalis*, R. E. Gereau and B. Manara for assistance with Latin composition, and P. Berry, B. Holst, and R. E. Gereau for critical comments.

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ARDISIA LUNDELLIANA, A NEW SPECIES OF MYRSINACEAE FROM PANAMA

The efforts of the Missouri Botanical Garden's plant exploration program in Panama continue to yield new and phytogeographically interesting taxa, even in areas as well known as western Panama. During routine identification of plants collected by Gordon McPherson, I discovered a hitherto undescribed species of *Ardisia*, which is described below:

Ardisia lundelliana Pipoly sp. nov. TYPE: Panama. Chiriquí: vic. Fortuna Dam, forested slopes along ridge at S boundary of watershed, 8°45′N, 8°15′W, 1,250 m. Tree 4 m; calyx brown; corolla pale pink; fr. green, 28 Apr. 1986, *G. McPherson 9107* (holotype, MO; photocopy, US). Figure 1.

Ob ramulos foliorum costas abaxiales necnon inflorescentiarum rhachides rufo-stellato-tomentosos et furfuraceo-stipitato-lepidotos, inflorescentias cernuas, flores subcorymbosos, pedicellos recurvatos, antheras lineo-lanceolatas et longitudinaliter dehiscentes *A. brenesii* arcte affinis, sed ab ea foliis praeclare petiolatis (non sessilibus), monomorphis (non dimorphis), ellipticis (non oblanceolatis vel obovatis nec oblanceolatis vel oblongis), basibus cuneatis (non auriculatis) atque apicibus acutis (non acuminatis), sepalis 5.2–6.0 (non 1.4–1.6) mm longis marginalibusque integerrimis (non erosis), petalisque 12.0–13.9 (non 3.9–4.5) mm longis, intus prope basin verrucosis (non laevis) statim cognoscitur.

Tree to 4 m, the branchlets, petioles, abaxial leaf costae, inflorescence rachis, pedicels and calyx rufous-stellate tomentose and furfuraceous stipitate-lepidote. Leaves petiolate, the petioles marginate, (1.1–)1.5–2.0 cm long, the blades coriaceous, elliptic, (7.0–)11.0–16.7(–18.0) cm long, (4.0–)-5.2–7.7 cm wide, apically acute, basally cuneate, glabrous above, densely furfuraceous stipitate-lepidote below, the margins entire, revolute. Inflorescence terminal, pendent, paniculate, 8.0–15.0 cm long, the peduncle 2.3–2.7 cm long, the rachis linear in flower, becoming flexuous in fruit. Flowers corymbose; pedicels terete, 0.6–1.4 cm long; sepals erect, coriaceous, dextrorsely contorted, widely ovate, 5.2–6.0 mm long, 3.6–4.0 mm wide, apically acute, asymmetric, basally auriculate on one side, the auricle and margin scarious, glandular-ciliate, densely rufous stellate and furfuraceous lepidote without, sparsely stipitate-lepidote basally within, black lineate-punctate; petals reflexed at anthesis, chartaceous, lanceolate, 12.0–13.9 mm long, 3.9–4.5 mm wide, apically attenuate, slightly asymmetric, glabrous, densely black punctate and lineate-punctate, pink, verruculose basally within, the margin white, subentire, irregular; stamens 10–12.5 mm long, the filaments hyaline, 6.0–6.3(–6.9) mm long, glabrous, the anthers linear-lanceolate, concolorous, 4.0–5.9 mm long, apically apiculate, basally sagittate, dorsifixed, the connective inconspicuously black-punctate dorsally, longitudinally dehiscent; ovary globose, 5.3–5.7 mm tall, 3.0–3.1 mm diam., densely orange-punctate; style 9.1–9.4 mm, exserted at anthesis, eccentric or not, densely and prominently orange-punctate; stigma punctiform; placenta globose, obtuse apically, 1.2–1.3 mm long and in diameter, the ovules 19–24, pluriseriate. Fruit globose, 5–7 mm diam. (immature), prominently verrucose, inconspicuously punctate.

Ardisia lundelliana belongs to a group of species often referred to the genus *Auriculardisia* Lundell. Because the salient features defining this group (Lundell, 1981) have been encountered in a number of paleotropical members of the more broadly defined *Ardisia* Swartz, this species is assigned to *Ardisia* until a more thorough, pantropical survey is completed (Pipoly & Stone, in prep.). With rufo stellate-tomentose abaxial leaf midribs, inflorescence rachises and branchlets, pendent, subcorymbose flowers on panicles, and linear-lanceolate and longitudinally dehiscent anthers, *A. lundelliana* is clearly most closely related to *A. brenesii* (including *A. limonensis* Lundell). However, *A. lundelliana* is readily separable by its petiolate (not sessile), monomorphic (not dimorphic), and elliptic (not oblanceolate or obovate) leaves with cuneate (not auriculate) bases and acute (not acuminate) apices. Floral characters allowing easy recognition include the longer, entire sepals

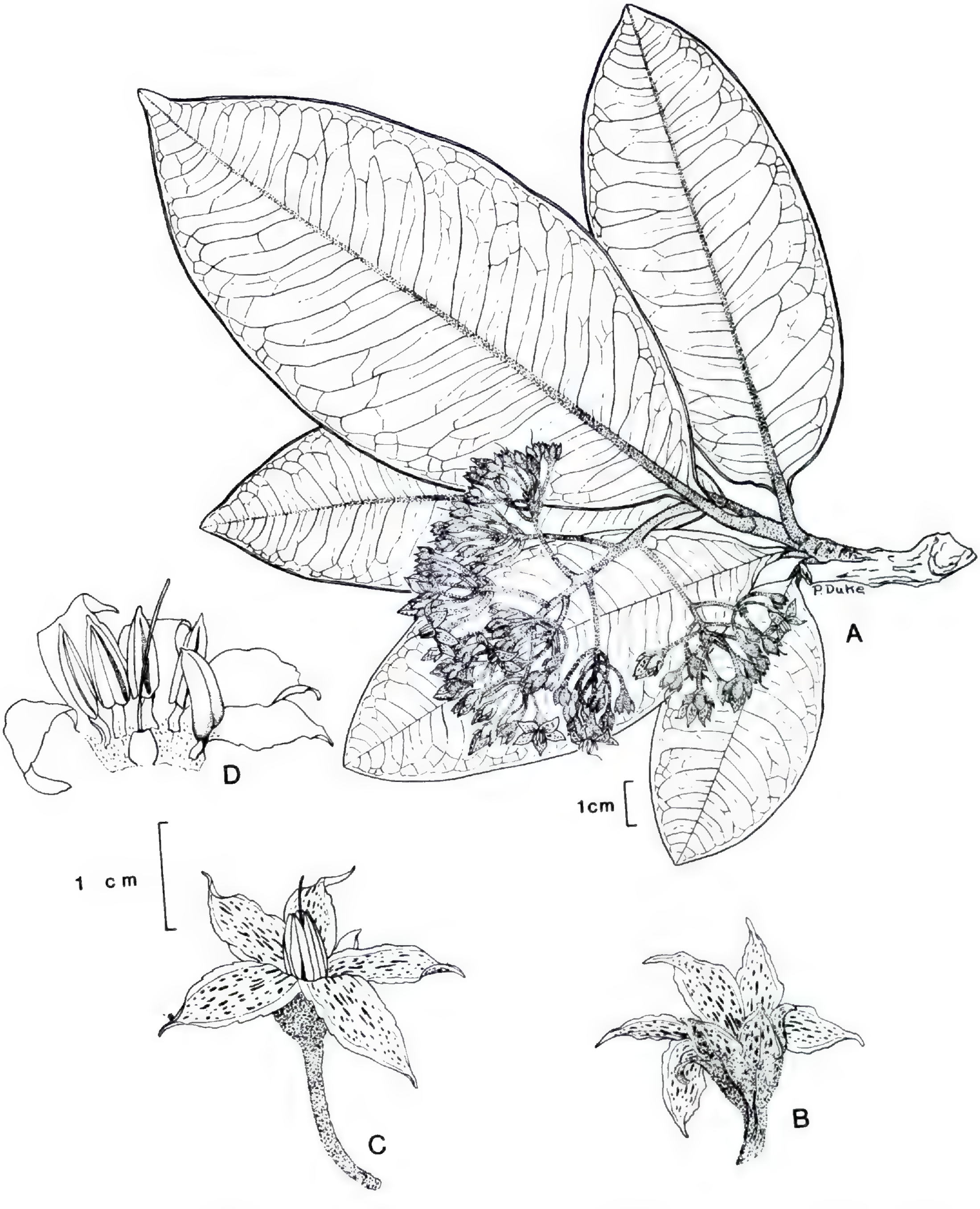

FIGURE 1. *Ardisia lundelliana* Pipoly.—A. Branchlet, showing pendent inflorescence, tomentose costae.—B. Calyx, showing hyaline, entire margin.—C. Flower, at anthesis.—D. Dissected flower, showing another dehiscence and adaxial corolla surface basally verrucose. (A–D drawn from holotype, *McPherson 9107*, MO.)

and longer, verrucose petals. Among these characters, a preliminary survey revealed that the verrucose petals represent an autapomorphic character state.

The dimorphic leaf character present in *A. brenesii* refers to the production of modified leaves axillant to the inflorescence of that species, a feature thought to autapomorphic to it (Pipoly, submitted). Ecologically, *A. brenesii* is restricted to riparian areas in tall wet forest or moist premontane forest, whereas *A. lundelliana* is a montane forest, ridge-top species. Clearly, much more exploration

of western Panama (especially the Atlantic slope) is needed, because this and some 50 other species of *Ardisia* collected from there are known only from their type specimens.

It is with great pleasure that I dedicate this species to Cyrus Longworth Lundell, who has just completed his sixtieth year of research in Mesoamerican Myrsinaceae.

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PELTOSTIGMA PARVIFLORUM (RUTACEAE), NUEVA ESPECIE DE COSTA RICA Y COLOMBIA

La tribu Zanthoxyleae (Rutaceae: Rutoideae) está constituida por un grupo de subtribus laxamente vinculadas entre sí y de afinidades dudosas (Waterman, 1975). Esta tribu incluye la subtribu Choisyinae, compuesta por cinco pequeños géneros con poca cohesión geográfica, de los cuales dos, *Choisya* Kunth y *Peltostigma* Walp., figuran en la flora neotropical (Engler, 1931). *Choisya* tiene siete especies desde el suroeste de los Estados Unidos hasta el sur de México (Muller, 1940), mientras que *Peltostigma* contaba hasta ahora con dos especies de Jamaica y desde el noroeste de México (estados de Durango y Sinaloa) hasta Costa Rica (Morton, 1933; Standley & Steyermark, 1946; F. Chiang, com. pers.) que son notables por sus flores grandes y muy fragantes. Los programas de colección botánica en Costa Rica y Colombia y el estudio de ejemplares en los herbarios CR, HUA, y MO han dado como resultado el descubrimiento de una nueva especie de *Peltostigma*, muy semejante a las precedentes en su arquitectura floral pero diferenciada de éstas por sus hojas unifolioladas y el tamaño muy reducido de sus flores.

Peltostigma parviflorum Q. Jiménez & Gereau, sp. nov. TIPO: Costa Rica, Prov. San José, 9°43′10″N, 84°23′10″W, Zona Protectora La Cangreja, Santa Rosa de Puriscal, 400–500 m, 4 septiembre 1987 (fl), *Q. Jiménez M. & L. J. Poveda A. 494* (holotipo, CR; isotipos, F, K, MO). Figura 1.

Frutices arboresque 1–11 m alti, plerumque ramosissimi, cortice obscuro, partibus vegetativis omnibus glabri. Folia unifoliolata; petiolo (petiolulum pulvinatum includenti) 0.2–5.6 cm longo, adaxialiter canaliculato, interdum anguste alato; lamina ovato-elliptica usque ovato-oblonga, 3.2–20.6 × 1.2–10.2 cm, apice obtusa usque acute acuminata, basi rotunda usque cuneata, margine integra usque leviter sinuata, submembranacea usque chartacea, utrinque glanduloso-punctata; nervis secundariis 6–8 ante marginem anastomosantibus; nervis intersecundariis ex tertiariis subparallelis laxe reticulatisve vix diversis. Inflorescentiae axillares solitariae vel hae 2–5 fasciculos formantes; pedunculis 1- usque 3(–5)-floris, unifloris interdum pari bractearum minutarum munitis; pedunculo (1–)3–38 mm longo, glabro; pedicello 0–21 mm longo, glabro usque minute puberulo. Flos sepalis 3 pallide viridibus, late ovatis usque suborbicularibus, subaequalibus, 2.4–3.0 × 2.3–2.9 mm, abaxialiter glabris usque puberulis, ciliolatis; petalis 3 albis cremeisve, in vivo concavis conchiformibusque, in sicco late ovatis usque suborbicularibus, 8.2–10.1 × 8.0–9.7 mm, ciliolatis; disco nectarifero carnoso, lobulato, coacto, aurantiaco; staminibus 10–12 inaequalibus filamentis arcuatis antherisque super stigmata contiguis; filamentis albis, linearibus, alatis; antheris luteis, ovoideis, thecis basi parum divergentibus; ovario pubescenti ex segmentis 6 rhomboideis basi tantum connatis constanti; stylis subterminalibus 0.5–0.7 mm longis; stigmatibus luteis in massam unam obloideam coalitis; ovulo in quoque segmento ovarii solitario. Fructus ex mericarpiis 2–6 primum basi connatis puberulisque maturitate distinctis glabrisque constans; mericarpiis oblique ellipsoideis, 1.5–2.1 × 0.6–1.1 cm; endocarpio luteo cum semine caduco; semine in quoque mericarpio solitario, fusiforme-ellipsoideo, papilloso, arillodio membranaceo latere hilari munito.

Arbustos y árboles 1–11 m de alto, hasta 12 cm de DAP, usualmente muy ramificados, la corteza oscura, las partes vegetativas glabras. Hojas unifolioladas; pecíolo 0.2–5.6 cm incluyendo el peciólulo pulvinado), adaxialmente acanalado, ocasionalmente angostamente alado; lámina ovado-elíptica a ovado-oblonga, 3.2–20.6 × 1.2–10.2 cm (L/A = 2.0–2.9), el ápice obtuso hasta acuminado y agudo, la base redondeada hasta cuneada, los márgenes enteros hasta levemente sinuados, submembranácea a cartácea, glanduloso-punteada por ambas caras; nervios secundarios 6–8, anastomosándose sin alcanzar el margen; nervios intersecundarios poco diferenciados de los terciarios, éstos subparalelos hasta laxamente reticulados. Inflorescencias axilares, solitarias o en fascículos de 2–5; pedúnculos 1- a 3(–5)-floros; pedúnculos unifloros con o sin un par de brácteas menudas demarcando la base del pedicelo; pedúnculo (1–)3–38 mm, glabro; pedicelo 0–21 mm, glabro hasta menudamente puberulento. Sépalos 3, verde pálidos, anchamente ovados a suborbiculares, subiguales, 2.4–3.0 × 2.3–2.9 mm, abaxialmente glabros a puberulentos, ciliolados; pétalos 3, blancos a blanco-cremosos, cóncavos y conquiformes en vida,

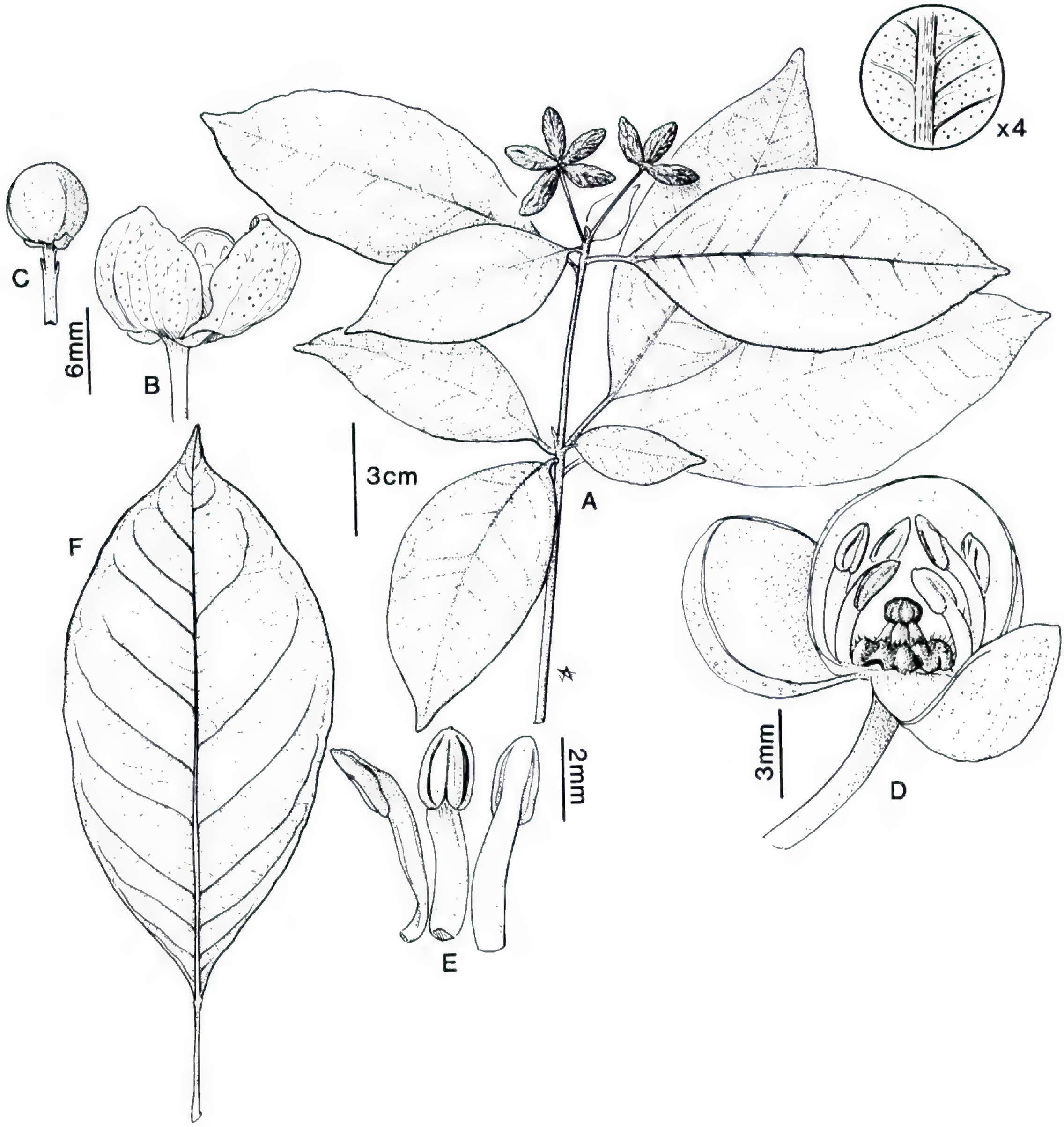

FIGURA 1. *Peltostigma parviflorum.*—A. Planta en fruto.—B. Flor.—C. Botón floral.—D. Vista interior de una flor con una porción de dos pétalos y seis estambres eliminados.—E. Estambres en vista lateral, ventral y dorsal.—F. Hoja. (A de *Grayum et al. 4955*; B–E de *Jiménez et al. 710*; F del isotipo en MO).

anchamente ovados a suborbiculares cuando prensados, 8.2–10.1 × 8.0–9.7 mm, ciliolados; disco nectarífero carnoso, lobulado entre los segmentos del ovario, aterciopelado, anaranjado; estambres 10–12, algo desiguales, los filamentos arqueados y las anteras contiguas encima de los estigmas; filamentos 2.1–4.4 mm, blancos, lineares, alados y frecuentemente con el ápice de ancho subigual al de la antera; anteras ovoides con las tecas algo divergentes en la base, amarillas; tecas 1.5–2.1 × 0.5–0.9 mm; ovario pubescente, formado por 6 segmentos romboides unidos solamente en la base, los segmentos 1.4–1.7 × 0.7–0.9 mm; estilos subterminales, 0.5–0.7 mm; estigmas amarillos, unidos en una masa obloide, ésta 0.5–1.3 mm de alto, 1.0–1.5 mm de ancho; óvulo 1 en cada segmento. Fruto formado por 2–6 mericarpios unidos en la base, puberulentos cuando jóvenes, separados y glabros en la madurez; mericarpios oblicuamente elipsoides, reticuladamente rugosos en ejemplares en herbario, 1.5–2.1 × 0.6–1.1 cm; endocarpio amarillo, caedizo con la semilla; semilla 1 en cada

mericarpio, fusiforme-elipsoide, papilosa, 7.9–10.1 × 3.5–5.1 mm, con un arilodio (porción no lignificada del endocarpio) membranáceo a lo largo de su lado hilar.

Ejemplares adicionales examinados. COSTA RICA. GUANACASTE: Rancho Harold, región del Volcán Cacao, 30 julio 1986 (fl, fr), *I. A. & A. M. Chacón 2107* (CR, MO); 10°47′N, 85°18′W, Parque Nacional Rincón de la Vieja, above Hacienda Santa María, 900–1,200 m, 28 enero 1983 (fl), *Davidse et al. 23449* (CR, MEXU, MO); Parque Nacional Rincón de la Vieja, Hacienda Santa María, 800 m, 28 enero 1983 (fl), *Garwood et al. 796* (BM, CR, MO); 10°40′N, 85°03′W, Hacienda Montezuma, Volcán Tenorio, 600–700 m, 25 enero 1985 (fl), *Grayum et al. 4955* (CR, MEXU, MO); 10°48′N, 85°19′W, Parque Nacional Rincón de la Vieja, Hacienda Santa María, 750–850 m, 16 agosto 1987 (fr), *G. Herrera 716* (CR, MEXU, MO); Hacienda Santa María, carretera a Colonia Blanca, 600–750 m, 17 octubre 1987, *G. Herrera 882* (CR, MEXU, MO); 10°57′N, 83°28′W, Santa Cecilia, La Cruz, Estación Pitilla, faldas Cerro Orosilito, 700 m, 14 junio 1989 (fl), *Q. Jiménez M. et al. 710* (CR, MO). PUNTARENAS: 300 m N of Monteverde main road on Quebrada Máquina, ca. 1,400 m, 14 julio 1990 (fr), *Woodruff et al. 363* (CR, TEX). COLOMBIA. ANTIOQUIA: 5°53′N, 74°39′W, Mpio. San Luis, Cañón del Río Claro: sector occidental, margen izquierda, 325–400 m, 2 diciembre 1983 (fr), *A. Cogollo 1003* (HUA, MO); sector norte, margen izquierda, 340–500 m, 24 diciembre 1983 (fr), *A. Cogollo 1069* (HUA, MO); sector oriental, margen derecha, 325 m, 2 junio 1984 (fl), *A. Cogollo 1766* (HUA, MO); camino al Refugio, 600 m, 11 octubre 1982 (fl, fr), *E. Rentería et al. 2845* (HUA, MO).

Las poblaciones conocidas de *Peltostigma parviflorum* forman dos morfotipos según su posición geográfica: la "raza norteña" consiste en las colecciones citadas de Guanacaste y Puntarenas, Costa Rica; y la "raza sureña" consiste en el tipo y las colecciones citadas de Antioquia, Colombia. Las diferencias entre estas dos razas son las siguientes:

"raza norteña": hojas con pecíolos de 0.2–2.1 cm de largo y poco variables, el pecíolo mayor en un indivíduo dado sobrepasando al menor por 0.5–1.5 cm de largo; folíolo 3.2–16.0 × 1.2–7.3 cm, el ápice obtuso u obtusamente acuminado, la base aguda hasta redondeada; pétalos 8.2–9.3 × 8.0–8.5 mm.

"raza sureña": hojas con pecíolos de 0.3–5.6 cm de largo y muy variables, el pecíolo mayor en un individuo dado sobrepasando al menor por 2.0–4.5 cm de largo; folíolo 4.2–20.6 × 2.2–10.2 cm, el ápice agudamente acuminado y la base usualmente atenuada; pétalos 9.8–10.1 × 8.5–9.7 mm.

Aunque consistentes dentro de sus áreas geográficas, tales diferencias vegetativas podrían reflejar las condiciones ecológicas de las localidades, y la carencia de material con flores nos impide establecer una correlación significativa entre el tamaño de los pétalos y las características foliares. La "raza sureña" se encuentra en alturas de 325–600 m.s.n.m., y en Costa Rica habita el bosque tropical muy húmedo (Tosi, 1969) con clima muy húmedo caliente con una corta estación seca (Herrera, 1985), asociada con *Bauhinia manca* Standley (Caesalpiniaceae), *Coccoloba tuerckheimii* J. D. Smith (Polygonaceae), *Croton killipianus* Croizat (Euphorbiaceae), *C. schiedeanus* Schldl., *Hampea platanifolia* Standley (Malvaceae), *Hyperbaena leptobotryosa* (J. D. Smith) Standley (Menispermaceae), *Olmedia aspera* Ruíz López & Pavón (Moraceae), *Otoba novogranatensis* Mold. (Myristicaceae), *Paullinia rugosa* Benth. ex Radlk. (Sapindaceae), *Schizolobium parahybum* (Vell. Conc.) S. F. Blake (Caesalpiniaceae), *Turpinia occidentalis* Don (Staphyleaceae), *Unonopsis theobromifolia* Zamora & Poveda (Annonaceae) y *Vitex cooperi* Standley (Verbenaceae). La "raza norteña" habita en alturas de 600–1,400 m.s.n.m. en bosque tropical muy húmedo en transición a premontano y bosque pluvial premontano (Tosi, 1969) con clima húmedo caliente con una moderada estación seca (Herrera, 1985), frecuentemente asociada con otras Rutaceae (*Angostura nicaraguensis* (Standley & L. O. Williams) T. Elias, *Erythrochiton lindenii* Planchon, *Galipea granulosa* Kallunki, y *Stauranthus perforatus* Liebm.). En espera de más datos, especialmente medidas de partes florales, dejamos los dos "razas" sin reconocimiento nomenclatural.

Stauranthus Liebm. es un género de Rutaceae con dos especies anteriomente conocidas solamente de México (Standley, 1923). *Stauranthus perforatus* está actualmente conocida fuera de la República Mexicana por las colecciones siguientes:

COSTA RICA. CARTAGO: along Camino Raíz de Hule, SE of Platanillo (Tsipiri), 1,200–1,400 m, 1 julio 1976, *Croat 36799* (MO). PUNTARENAS: Reserva Biológica Monteverde, 8 agosto 1975, *L. J. Poveda 1112* (CR, MO). PANAMA. COCLÉ: hills above El Valle, ca. 1,000 m, 24 diciembre 1972, *Gentry 6874* (MO).

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TWO NEW SPECIES OF *TRIXIS* (ASTERACEAE–MUTISIEAE) FROM PARAGUAY

Two new species of *Trixis* are described from Paraguay. *Trixis cerroleonensis* Soria & Zardini from Occidental Paraguay is most similar to *T. ophiorrhiza* Gardn. but has much smaller phyllaries. *Trixis ravenii* Zardini & Soria from Oriental Paraguay is most similar to *T. spicata* Gardn. but has deltoid leaves decurrent at the base.

The genus *Trixis* (Asteraceae–Mutisieae) comprises 60 neotropical species ranging from the southern United States and Mexico to northern Chile, northern Argentina, and Uruguay. The genus is in need of revision; only local treatments are available (Anderson, 1972; Baker, 1884; Cabrera, 1936; Loja, 1969). During our exploration work in Paraguay, we have found two new species, which we describe here.

Trixis ravenii Zardini & Soria, sp. nov. TYPE: Paraguay. Amambay: Arroyo Estrella, 22°20'S, 56°20'W, 7 May 1989, *Soria, Bacigalupo & Fortunato 3825* (holotype, FCQ). Figure 1.

Herba 0.50–1 m. Caule partim alato inferne simplici, superne ramoso. Folia sessilia deltoidea denticulata, dorso dense breviter pubescentia supra laxa pilosa. Capitula spicata. Involucrum campanulatum 6–11 mm longum, bracteis lanceolatis dense pilosis, extimis paucis. Flores 5. Achenia cylindrica pilosa rostrata. Pappus albus.

Herbs 0.50–1 m tall, erect, the individual stems with few branches. Stems partially winged, 3–5 mm wide, pilose. Leaves sessile; blades 3–6 cm long, 2–6 cm wide, rhomboid or deltoid, acute, decurrent at the base, pilose below, sparsely pilose to hispidulous above; margins denticulate; midrib and nerves prominent below. Inflorescence spike-like. Accessory bracts 2–3, 5–8 mm long, 2–3 mm wide, lanceolate or ovate, acuminate, pilose below, convex, margin entire; midrib and nerves prominent above. Phyllaries in two series, the outside 2–3, 6–8 mm long, 2–3 mm wide, margin entire, acuminate, pilose below, midrib and nerves prominent below; the inside 5–6, 10–11 mm long, 2 mm wide, lanceolate to ovate, pilose below, margin entire, apex acuminate, midrib and nerves prominent above. Receptacle 4–5 mm wide. Florets 5. Tube of the corolla 5–6 mm long, 0.1–0.2 mm wide at the base, 1 mm wide at the mouth, glabrous or with few trichomes or glandular hairs; outer lip 1.5–2 mm long, 0.1 mm wide, glabrous or with few hairs, flat; lobes of the inner lip 1.5–2 mm long, 1–1.5 mm wide at the base, glabrous or with few trichomes at the apex. Filament 1.5–2 mm long. Anthers 4.5–5 mm long, appendages 0.5–1 mm long; thecae 2.5–3 mm long; tails 1–1.5 mm long. Style 5.5–6 mm long below the bifurcation, the branches 1–1.5 mm long. Achenes rostrate, 3–7 mm long, 0.3–0.5 mm wide, covered with glandular and nonglandular hairs. Pappus 7–9 mm long.

Trixis ravenii is a distinctive species, most similar to *Trixis spicata* Gardn. from Central Brazil, which has winged stems and oblong leaves.

We dedicate this species to Peter H. Raven for his efforts in institutionally establishing Paraguayan botany 10 years ago.

Trixis cerroleonensis Soria & Zardini, sp. nov. TYPE: Paraguay. Chaco: Cerro León, 8 Aug. 1983, *Hahn 1555* (holotype, PY; isotype, MO). Figure 2.

Frutex dense piloso et glanduloso. Caule haud alato. Folia sessilia ellipticis vel lanceolatis denticulata. Capitula corymbosa. Involucrum campanulatum 1.3–1.5 mm longum, bracteis linear-lanceolatis, extemis paucis. Flores 20–30. Achenia cylindrica pilosa rostrata. Pappus albus.

Shrubs 1–1.5 m tall, erect. Vegetative parts, accessory bracts and phyllaries with glandular and nonglandular hairs. Stems not winged, glandular and pilose; internodes (0.1–)0.5–1.5 cm long. Leaves subsessile; blades 2.5–10 cm long, 1.5–2 cm wide, usually elliptical or lanceolate to oblanceolate, acuminate, attenuate at the base, glandular and pilose above, glandular and sericeous below; margin denticulate; midrib and nerves prominent below. Inflorescence a corymb; peduncles 1–2.5 cm long, glandular and sericeous. Accessory bracts 5–6; 10–20 mm long, 2–6 mm wide, lanceolate

FIGURE 1. *Trixis ravenii* Zardini & Soria.—A. Habit, ×0.5.—B. Capitulum, ×8.—C. Flower, ×10.—D. Anther, ×10.—E. Style, ×10.—F. Achene × 10.

to oblanceolate or elliptic, acute, sessile or subsessile, glandular and pilose or sericeous on both surfaces, margin entire, flat. Phyllaries 10–12, 13–15 mm long, 1.5–2 mm wide, linear-lanceolate, acute, convex, with glandular and sericeous hairs. Receptacle with nonglandular hairs. Florets 20–30; tube of the corolla 6–7 mm long, glabrous or with glandular and sericeous hairs; outer lip 2.5 mm long, glabrous; lobes of the inner lip 2 mm long. Anthers 5–6 mm long, tails 2 mm long. Style

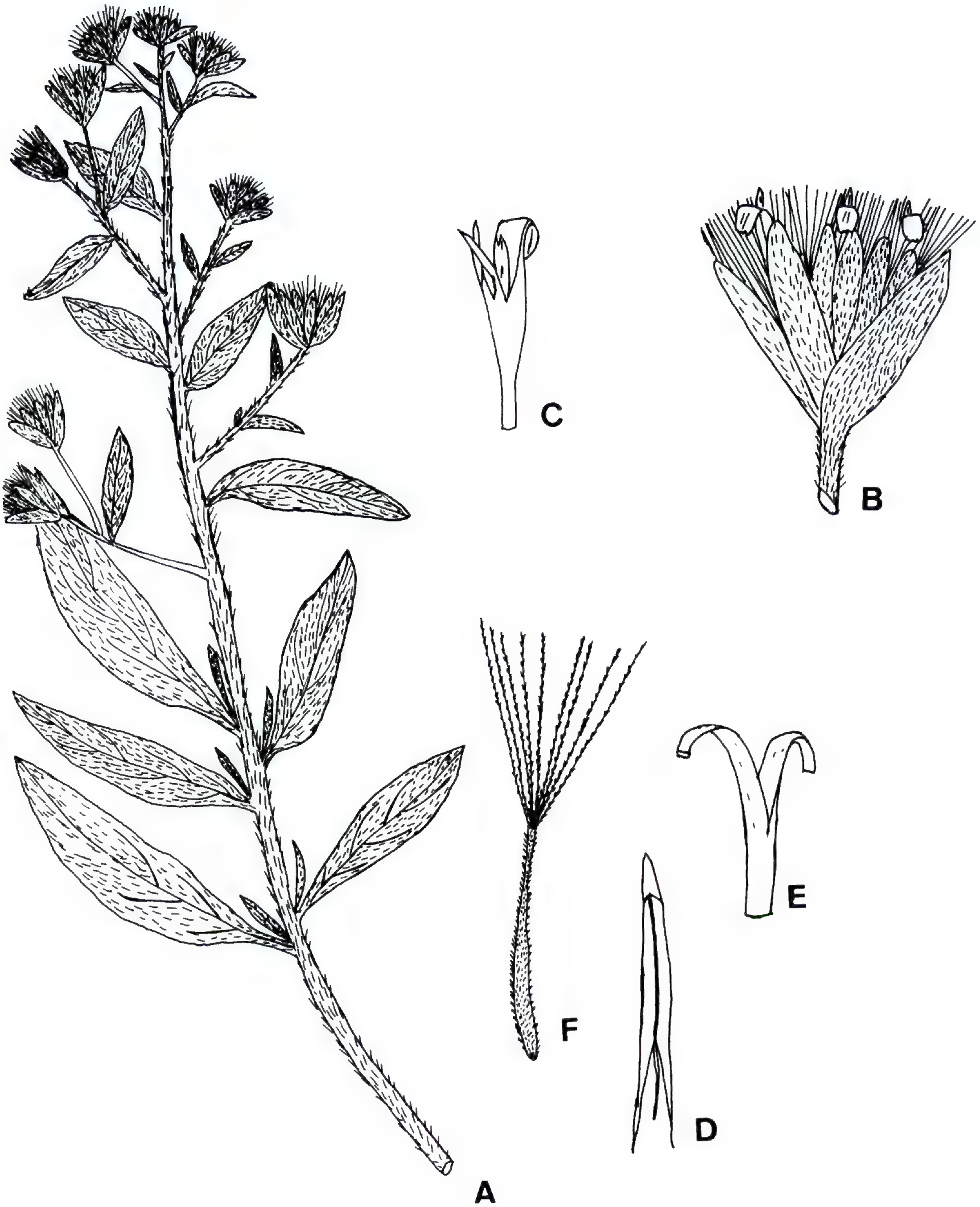

FIGURE 2. *Trixis cerroleonensis* Soria & Zardini.—A. Habit, ×0.5.—B. Capitulum, ×4.—C. Flower, ×5.—D. Anther, ×10.—E. Style, ×10.—F. Achene, ×10.

5 mm below the bifurcation, branches 1 mm long. Achenes 7 mm long, 0.5 mm wide, papillose, rostrate. Pappus white.

Trixis cerroleonensis is a distinctive species. It is most similar to *Trixis ophiorrhiza* Gardn. from Central Brazil, which has larger phyllaries.

We thank C. Jeffrey (K) for allowing access to photographs of the types, and Gloria Delmas and Adrian Eliceche for help with the illustrations.

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INTRASPECIFIC VARIATION IN *PAVETTA RIGIDA* (RUBIACEAE): ESTIMATES OF RELIABILITY OF TAXONOMIC INFORMATION

Variations in number of flower buds per inflorescence, number of inflorescences per plant, approximate plant height, leaf blade length and width ranges, number of secondary lateral leaf veins, and leaf length/width ratio are analyzed for a sample of 11 plants of *Pavetta rigida* near Lake Barumbi Mbo, Southwest Province, Cameroon. Lowest prevalence of bacterial leaf nodules is noted to coincide with lowest flower number among plants sampled. *Pavetta rigida* provides quantified evidence that, for purposes of plant identification, ranges of variation in individuals being identified and ranges of variation in keys and descriptions based on one or few collections can often be doubled in attempts to fit specimens being identified into existing taxonomic groups.

Pavetta L. (Rubiaceae subfamily Ixoroideae) is a paleotropical genus of ca. 400 species, mostly forest shrubs, having four-merous flowers, nonrecurved stigmas, and the "Ixoroid" pollination mechanism sensu Bremekamp (1934) and Robbrecht (1988). Eleven individuals of *P. rigida* Hiern subg. *Pavetta* were found in flower bud shortly before anthesis near a path around the perimeter of Lake Barumbi Mbo near Kumba, Southwest Province, Cameroon, inside the crater containing the lake. The distance between the farthest apart of the 11 individuals was estimated to be ca. 1 km straight line distance or nearly ¼ of the circumference of the lake. The nearest two individuals were separated by ca. 10 m.

Methods

Field recordings of the ranges of variation in the following characters were made from April 18 through April 23: numbers of flower buds per inflorescence in inflorescences nearing anthesis, numbers of inflorescences per plant, approximate plant heights, leaf blade lengths and widths, and numbers of lateral veins on one side of leaf midribs. Leaf length/width ratios were calculated later. Ranges and midranges of character states for individual plants, and the resulting total range in the plants studied, were determined from the data in Figure 1. The mean per-plant range was determined for each character and compared with the total range for the 11 plants in the study. Comparisons of the ranges of variation observed in this study were then made with earlier species descriptions of *P. rigida* (Hiern, 1877; Bremekamp, 1934).

Results for Quantitative Characters

Raw data are shown in Figure 1. Overall ranges, as well as means and standard deviations of the individual plant midranges, are presented in Table 1. Mean per-plant ranges are expressed as percentages of the total range of the 11 plants in Table 2. The comparisons of ranges of variation observed in this study with earlier species descriptions are presented in Table 3. Results presented in the figure and tables not thought to be self-explanatory are discussed below.

NUMBER OF FLOWER BUDS PER INFLORESCENCE

Flower buds were counted on each inflorescence nearing anthesis on each of the 11 plants. Three plants had one such inflorescence, seven had two such inflorescences, and one had four such inflorescences. The mean of the midranges in number of flowers per inflorescence on each individual of 82.4 buds and standard deviation of 32.6 buds (Table 1) do not fully express the pattern of variation in this character. Of the 11 plants, five had all inflorescences nearing anthesis with 86–124 flower buds, five had all with 50–72 buds, and one had all with 19–41 buds. The 11 plants can thus be divided into three nonoverlapping groups with regard to number of flowers per inflorescence. If the original species description had included number of flowers per inflorescence and had been based on any one of these plants, the probability that the

TABLE 1. Total character state ranges, means, and standard deviations in 11 individuals of *Pavetta rigida*.

Character	Range	Mean of mid-ranges for individual plants	Standard deviation of mid-ranges for individual plants
Number of buds per inflorescence	19–124	82.4	32.6
Number of inflorescences per plant	1–5	—	—
Number of lateral veins[1]	6–15	9.6	1.0
Leaf blade length, cm	14–48	29.0	3.2
Leaf blade width, cm	5–17	11.5	1.4
Leaf blade length/width ratio	2.1–3.2	2.6	0.4
Plant height, m	1.0–2.5	—	—

[1] Only 10 plants scored for this character.

second plant found, even if in the same area, would have matched the description would have been less than 0.5. The original description (Hiern, 1877) did not mention this character and Bremekamp (1934), in his monograph of *Pavetta*, indicated flowers to be "circ. 100."

NUMBER OF INFLORESCENCES PER PLANT

As seen in Figure 1, almost two-thirds of the plants bore two inflorescences. Nearly, but not quite all, of the inflorescences were nearing anthesis.

NUMBER OF LATERAL VEINS ON ONE SIDE OF MIDRIB

Lateral veins included in these counts are only those veins originating at the midrib and extending all the way to a submarginal position on the leaf blades and larger in diameter than other veins originating from the midrib—i.e., secondary veins sensu Hickey (Hickey, 1973) originating from the midrib. This character was determined for each of 10 individuals.

LEAF BLADE LENGTH/WIDTH RATIO

This ratio was determined for each of the 11 plants as the midrange of leaf blade lengths divided by the midrange of leaf blade widths. The within-plant ratios so determined were scored to find the overall range in leaf length/width ratios.

PLANT HEIGHT

Plant height was estimated to the nearest 0.25 m.

COMPARISON WITH EARLIER SPECIES DESCRIPTIONS

As shown in Table 3, earlier species descriptions encompass considerably less than the complete range of variation revealed by measurements of 10 or 11 plants in all characters for which there are comparable data; the present study of 11 individuals failed to detect the complete range of variation known in plant height and leaf blade length.

OBSERVATION OF FEWER FLOWERS ON PLANT WITH PAUCITY OF BACTERIAL NODULES

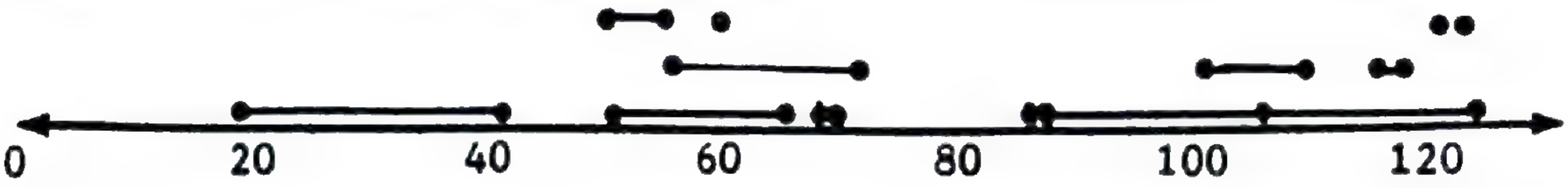
The one plant (voucher: *Manning 1777* MO) whose two inflorescences had the least flowers (41 and 19) was also the plant with least extensive leaf growths, termed bacterial nodules (Bremekamp, 1934; Lersten & Horner, 1976) or leaf galls (Robbrecht, 1988), characteristic of most *Pavetta* species. These growths were not prevalent on the plant and individual leaves sometimes lacked them, unlike all the other individuals in this survey. This

TABLE 2. Ranges of variation in individual plants compared to total range of variation in 11 plants.

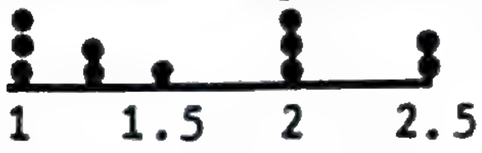
Character	Range of ranges in individuals	Mean range per individual	Total range of 11 plants	Mean % of total range per individual
Number of buds per inflorescence[1]	1–38	13.5	105	13
Number of lateral veins	3–7	5.3	10	53
Leaf blade length, cm	10–29	17.9	34	53
Leaf blade width, cm	4.5–11	6.6	12	55

[1] Only eight plants were included for this character because the other three had only one near-anthesis inflorescence each.

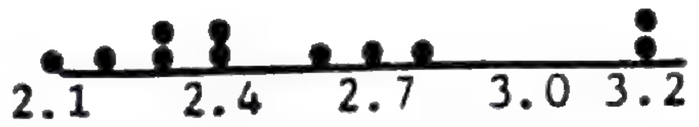
A. Numbers of flower buds per inflorescence. Inflorescences on the same plant are connected by horizontal lines.



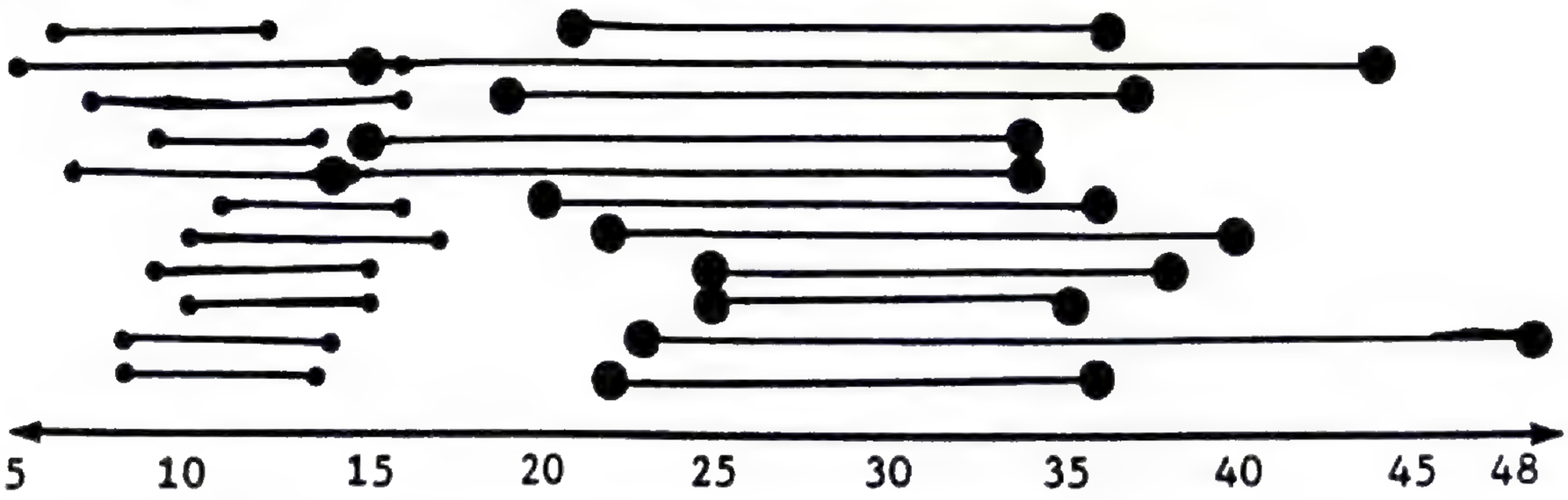
B. Plant heights, m.



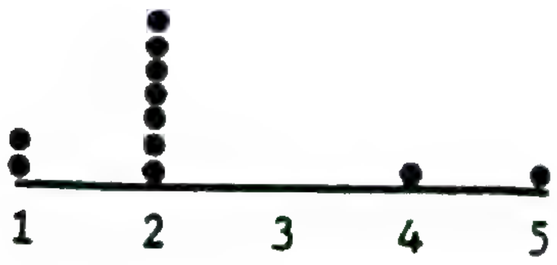
C. Leaf length/width ratios



D. Leaf lengths (●—●) and widths (●——). Each horizontal line represents the range in length or width for one individual in cm. Length and width ranges are shown side by side for each individual.



E. Numbers of inflorescences per plant



F. Ranges in numbers of lateral veins on one side of midrib. Each horizontal line represents one individual.

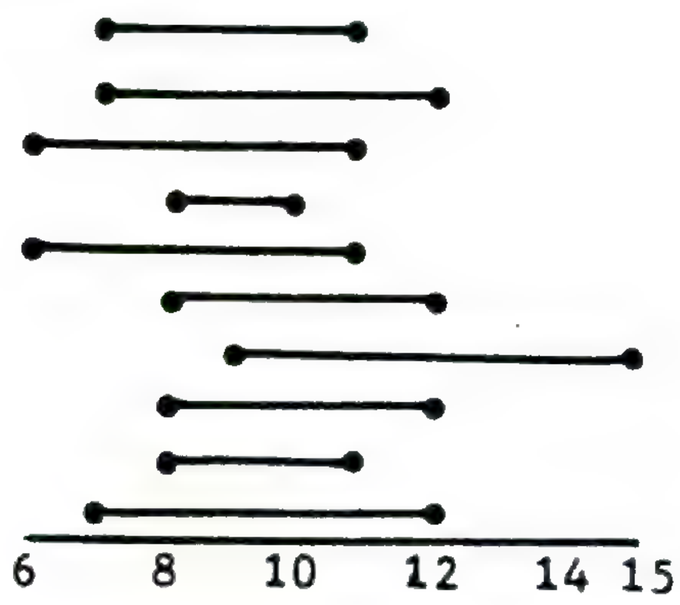


FIGURE 1. Intraspecific variation in selected characters of 11 individuals of *Pavetta rigida*.

plant appeared otherwise normal. The possible function of these nodules has been a topic of considerable interest (Lersten & Horner, 1976). To the possible functions may now be added promotion of initiation and development of increased numbers of flowers.

DISCUSSION AND CONCLUSIONS

Only 13.5/105, or ca. ⅛, of the total range in numbers of flower buds per inflorescence in this geographically limited sample of *Pavetta rigida* was typically expressed in single individuals with

TABLE 3. Comparison of ranges of variation stated for *Pavetta rigida* in its original and amended descriptions and from recent field measurements on 11 individuals with total reported ranges from all three sources. Blanks mean no data available. Hiern data converted to metric units from original.

Character	Range from Hiern (1877)		Range from Bremekamp (1934)		Range from author		Total range reported
	Raw	% of total	Raw	% of total	Raw	% of total	
Number of lateral veins	10–12	30	8–11	40	6–15	100	6–15
Leaf blade length, cm[1]	12.7–21.6	25	15–24	25	14–48	96	12.7–48
Leaf blade width, cm	6.75–8.5	15	7.5–11	29	5–17	100	5–17
Leaf blade length/width ratio	2.5		2.1		2.1–3.2	100	2.1–3.2
Plant height, m	3.0–3.7	26			1.0–2.5	56	1.0–3.7

[1] Hiern leaf blade lengths obtained by subtracting petiole lengths from leaf lengths.

more than one inflorescence. This cautions against using flower number as a defining character when delimiting taxa or creating keys based on few specimens.

For vegetative characters, ca. ½ of the total range of variation of this sample of *P. rigida* was typically expressed in individuals (53% for number of lateral veins, 53% for leaf blade length, and 55% for leaf blade width). Examination of herbarium specimens may thus actually reveal less than ½ of the total range of a similar sample for these characters, and ranges of variation in leaf characters stated in descriptions based on single or few collections should perhaps be at least doubled by users of keys and descriptions to best estimate true ranges of variation. There is also significant variation among individuals in each of the other characters surveyed.

The plants examined for this study, taken from a limited geographical area, may be reproductively within the same population. They cover a minute fraction of the geographical range of the species, which has been reported from Bioko Island, Equatorial Guinea, and a fairly large portion of the forested area of Cameroon. Thus, the results of this study may still understate the actual range of variation in characters surveyed. Table 3, comparing results of this study with observations of earlier workers, indicates this to be the case for plant height.

Often keys and descriptions of tropical plants are difficult to use at species and infraspecies levels because their character state ranges do not exactly fit specimens under study. It then becomes necessary to judge whether (1) the plant at hand represents an extension in the range of a particular character state, in which case the specimen may be referred to a previously described taxon; (2) the plant represents a new taxon; or (3) the user has made an earlier error in identifying the plant. The results reported here emphasize that at least for certain quantitative characters, the first of the three possibilities is to be expected.

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Cover illustration. *Ticodendron incognitum* Gómez-Laurito & Gómez P., by John Myers.

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A REVISION OF *ANTHURIUM* SECTION *PACHYNEURIUM* (ARACEAE)[1]

Thomas B. Croat[2]

ABSTRACT

This is the first published revision of *Anthurium* sect. *Pachyneurium* since that of Engler in 1905. Section *Pachyneurium* is one of 19 sections (all but one of which were treated by Engler, 1905, in his revision of *Anthurium*). The section consists of 114 species representing 126 taxa in two series, series *Pachyneurium* Schott, and the new series *Multinervia* Croat, with 110 and 16 taxa respectively. Forty-eight taxa (including nine subspecies or varieties) are described as new.

Section *Pachyneurium* is one of 19 recognized for *Anthurium* and is perhaps the most easily recognizable and well-defined group in the genus. It was for this reason, despite its size and taxonomic difficulty, that this section was chosen as a starting point for a revision of the genus. Section *Pachyneurium* is generally defined by its frequently rosulate or "bird's-nest" habit, its short, densely rooted caudex, the commonly short-petiolate, oblanceolate to obovate, mostly coriaceous leaf blades with usually free-ending primary lateral veins and, most importantly, the involute vernation (rolled inward from both margins) of the developing leaves (Fig. 1). All other sections of *Anthurium*, and indeed all other genera of Araceae (except *Lagenandra*), have convolute vernation (Fig. 2), with one margin rolled inward toward the midrib and the other margin rolled around the midrib and the rolled up opposite margin (like a continuous coil in cross section).

The section consists of two series with most species in series *Pachyneurium*. The other series, *Multinervia*, is restricted to the Andes of South America, especially in Ecuador. Series *Pachyneurium* contains all the species originally included in grex *Pachyneurium* by Schott (1860), and most of those included by Engler (1905) in sect. *Pachyneurium*. Series *Multinervia* contains species unknown to Schott and mostly unknown to Engler. The few species of series *Multinervia* treated by Engler were incorrectly placed in sect. *Polyneurium* or in sect. *Urospadix*, the latter having been employed by Engler as a rather broad "dumping ground." See Appendixes 1 and 2, respectively,

[1] This study was completed with support from National Science Foundation grants DEB 80-11649 and BSR 8306297. Support for publication was provided in part by National Science Foundation grant BSR-8914018.

[2] P. A. Schulze, Curator of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

for the ultimate disposition of species treated in sect. *Pachyneurium* by Schott and by Engler. See Appendix 3 for the disposition of all currently recognized *Pachyneurium* species and their sectional placement in the revisions of both Schott and Engler.

Methods and Materials

This revision was based on field studies in Central America between 1967 and 1979 and in South America in 1969 (Colombia), 1972 (Peru), 1976 (Colombia and Ecuador), 1980, 1983, 1984 (western South America), 1984 (Venezuela), and 1986 (western South America and Brazil). All but 28 of the 125 taxa were studied live or are under cultivation at the Missouri Botanical Garden. Except for those so indicated, all descriptions can be assumed to have been prepared from both living and dried material. Morphological characters were coded directly into a computerized database to ensure parallel and sortable descriptions. The aroid descriptions database contains 228 characters that are used to describe the morphological diversity expressed by *Anthurium*. The database also provides a means of sorting species by characters for writing keys, as well as for compiling lists of various character states. In addition, the database can be put to future use for identifications and for additions of new species for other treatments. The description file is directly tied to a nomenclatural database containing all species names and publication data for all Araceae species stored in Tropicos (Crosby, 1986; Crosby & Magill, 1986). Each species is represented by a unique number, which ties it to data in other files associated with the species. Discussions and exsiccatae are also stored in separate files, as are synonyms, but all parts are automatically reassembled for the final treatment. Herbarium specimens can be added to the exsiccatae database at any time and sorted in a standardized manner before being printed out. Thus, exsiccatae records can be added up to the last moment, even when the manuscript has been completed. Species descriptions are decoded into narrative text automatically from the descriptor base and require only minor editing to put them in a publishable form. Final treatments may be saved on hard disk or stored on tape, but the coded description data (which use very little core storage space) are a part of the permanent Tropicos database and can be used for other projects such as floras or ecological studies.

The terminology and usage in the descriptions in this paper are defined by Croat & Bunting (1979). The color of the spadix, unless otherwise indicated, refers to the color at anthesis, i.e., when the spadix is producing stigmatic droplets or when fresh stamens are emerging. Colors referenced in the descriptions that follow are taken from the color chart by Berlin & Kay (1969). This is hereafter cited as B & K. This color chart, available from the University of California Press, is a reproduction of the Munsell Color Array of 40 hues, at maximum saturation, with nine degrees of brightness. The B & K color chart represents 40 hues in the vertical columns and nine degrees of brightness in the horizontal rows. Colors are arranged in 10 basic clusters with four different hues per cluster, ranging from red through yellow, green, blue, purple, and finally red-purple. The four columns for each color cluster are numbered 2.5, 5, 7.5, and 10. These numbers are repeated for each basic color type. The colors from the B & K color chart are read by first reporting the color, then the row followed by the column. For example, the third color in the fifth row in the red area would be called Red 5/7.5. The second color in the eighth row would be called Red 8/5.

All estimates of ecological zones given in this paper are based on either Holdridge Life Zone maps for most Central American countries and for Panama or on the "Mapa de tipos de vegetación de la República Mexicana" (Flores et al., 1971). As yet no study has been made to correlate the vegetation types represented on the Mexican map with those of the Holdridge Life Zone system. For an understanding of the latter system, see Holdridge et al. (1971). For South America, maps based on the Holdridge System were used for Bolivia, Colombia, Ecuador, Peru, and Venezuela.

Mention should be made of the distribution of herbarium material of Araceae under cultivation. Herbarium material may consist of one of three kinds: (1) fertile original (wild) collections; (2) sterile original collections with an inflorescence added from the cultivated plant of the same number (generally the same individual from which the field specimens were made); and (3) material collected entirely from the cultivated plant. Specimens based entirely or in part on cultivated material are clearly indicated as such in herbaria.

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History of Section *Pachyneurium*

The first species of sect. *Pachyneurium* as it is recognized here was described by Linnaeus (1763) in *Species Plantarum* as *Pothos crenata*, and was transferred to *Anthurium* by Kunth in 1841. Three other species clearly belonging to sect. *Pachyneurium* were described in the genus *Pothos: Pothos crassinervia* was described by Jacquin in 1793 and transferred to *Anthurium* by Schott in 1832. The other two were *Pothos solitarius* Vell. Conc. described in 1829, and *P. maxima* Desf., described in 1832. The former was transferred to *Anthurium* by Schott in his *Prodromus* (1860), while the latter was transferred to *Anthurium* by Engler in 1905 and is here treated as a nomen dubium owing to the inability to place it with certainty in any currently recognized species. The genus *Pothos* as now circumscribed is restricted to Africa and Asia, especially Southeast Asia. Modern suprageneric classifications do not place *Pothos* close to *Anthurium*. Grayum (1984) places it in a separate tribe, Potheae in the subfamily Pothoideae. Grayum considers *Anthurium* isolated but closer to *Pothos* than to any other genus. He places *Anthurium* in a separate tribe Anthurieae in the same subfamily. Bogner & Nicolson (in press) remove *Anthurium* from the Pothoideae altogether and place it in the subfamily Lasiodeae, leaving *Pothos* in the Pothoideae with only two other closely related genera, *Pedicellarum* and *Pothoidium*.

The epithet *Pachyneurium* was first used in 1860 by H. W. Schott in his first revision of the Araceae in *Prodromus Systematis Aroidearum*. Although no *Anthurium* species were treated in his earlier *Synopsis Aroidearum* in 1856, 20 species were treated in the *Prodromus*. Half of these were described by Schott himself in that work or in earlier works during the previous decade. Others were described by Karl Koch or Frederick Liebmann during the same decade. In addition to the four species described as *Pothos* mentioned above, only one species of sect. *Pachyneurium*, *A. crassinervium* (Jacq.) Schott (described as *Pothos crassinervia* in 1793), was described before the early 1850s. Three of the 20 names included in Schott's 1860 revision, namely *A. acaule* (Jacq.) Schott, *A. hookeri* Kunth and *A. aduncum* (Vell. Conc.) Schott, were published before 1850 but these have been excluded from *Pachyneurium* and placed in other sections (see Appendix 1).

Of the remaining *Pachyneurium* names in Schott's 1860 revision, only nine species remain. These include *A. wagenerianum* K. Koch & Bouché, *A. fendleri* Schott, *A. spectabile* Schott, *A. crassinervium* (Jacq.) Schott, *A. affine* Schott, *A. schlechtendalii* Kunth, *A. crenatum* (L.) Kunth (erroneously treated by both Schott and Engler as *A. acaule* (Jacq.) Schott (Mayo, 1982)), *A. dombeyanum* Brongn. ex Schott, and *A. solitarium* (Vell. Conc.) Schott. Still other species of sect. *Pachyneurium* were described in Schott's revision,

but these he included in other groups (termed "greges" by Schott). These included *A. protensum* Schott (included in grex *Erythropodium*), *A. oxypum* Poeppig and *A. consobrinum* Schott (grex *Oxycarpium*), and *A. oerstedianum* Schott (including its synonym, *A. cuspidifolium* Schott) in grex *Xialophyllium*. Thus, a total of 13 species of *Pachyneurium* were included in Schott's revision, even though some were not recognized as such.

In Engler's 1905 revision, 62 names were included in sect. *Pachyneurium* (Appendix 2). Of this total, only 18 species were actual *Pachyneurium* species not already included in Schott's revision. Fourteen of the names included by Engler (in reality only 12 species, since two were synonyms), including *A. hookeri* Kunth, *A. hacumense* Engl., *A. weberbaueri* Engl., and all species numbered 52 through 62, have subsequently been proven to be non-*Pachyneurium* (see Appendix 2). Ten names included by Engler were synonyms of earlier names in Schott's revision, three names were synonyms of older names in Engler's own revision and four names have been excluded because of confusion in the nomenclature (see Species Excluded section). These are *A. maximum* (Desf.) Engl., *A. cymatophyllum* K. Koch & Sellow, *A. agnatum* Schott, and *A. tricarinatum* Sodiro.

In addition to the 18 species that Engler added to those Schott had included in his grex *Pachyneurium*, Engler included the following elsewhere: *A. oxycarpum* (sect. *Oxycarpium*), *A. pallatangense* Engl. (sect. *Polyneurium*), *A. oerstedianum* Schott (including *A. cuspidifolium* Schott, in sect. *Urospadix*, series *Obscureviridia*), *A. linguifolium* Engl. (sect. *Urospadix*, series *Flavescentiviridia*), and *A. spathiphyllum* N. E. Br. (sect. *Episeiostenium*). Of these, only *A. pallatangense* and *A. linguifolium* had not been treated by Schott.

Thus, in the 45 years between the publication of Schott's revision in 1860 and Engler's treatment for *Das Pflanzenreich* in 1905, an additional 22 valid species were described, bringing the total number of *Pachyneurium* species to 33. The species included by Engler, but not by Schott, in the present concept of sect. *Pachyneurium* were as follows (in the order presented in the revision):

A. pendulifolium N. E. Br.
A. paraguayense Engl.
A. joseanum Engl. (= *A. protensum* Schott)
A. jenmanii Engl.
A. uleanum Engl.
A. tarapotense Engl.
A. cubense Engl.
A. leonianum Sodiro
A. acutifolium Engl.
A. latissimum Engl.
A. barclayanum Engl.
A. ernestii Engl.
A. salviniae Hemsley
A. lindmanianum Engl.
A. martianum K. Koch & Kolb
A. selloum K. Koch
A. pallatangense Engl.
A. linguifolium Engl.

Until recent times, relatively few taxa of *Pachyneurium* had been described subsequent to Engler's revision. A list of the names published subsequent to Engler's time and prior to the beginning of this work is presented here:

A. agoyanense Sodiro = *A. dombeyanum* Brongn. ex Schott
var. *agoyanense* (1905) = *A. dombeyanum* Brongn.
var. *eleutheroneuron* Sodiro (1905) = *A. dombeyanum* Brongn.
A. angustilaminatum Engl.
var. *albidum* Sodiro (1906) = *A. angustilaminatum* Engl.
var. *brevipes* Sodiro (1906) = *A. angustilaminatum* Engl.
var. *crassum* Sodiro (1906) = *A. angustilaminatum* Engl.
var. *gladiatum* Sodiro (1906) = *A. angustilaminatum* Engl.
A. atropurpureum R. Schultes & Maguire
var. *atropurpureum* (1953)
var. *apertum* R. Schultes (1954) = *A. bonplandii* R. Schultes & Maguire subsp. *bonplandii*
A. bonplandii Bunting (1975)
A. concolor K. Krause (1932)
A. fasciale Sodiro (1905)
A. giganteum Matuda (1950) = *A. salviniae* Hemsley
A. guayanum Bunting (1975) = *A. bonplandii* Bunting subsp. *guayanum* (Bunting) Croat
A. lanjouwii Jonker & Jonker (1966)
A. maguirei A. Hawkes (1948)
A. ottonis K. Krause (1932)
A. rodrigoi A. Hawkes (1948) = *A. paraguayense* Engl.
A. superbum Madison (1978)
A. tessmannii K. Krause (1932) = *A. uleanum* Engl.
A. wurdackii Bunting (1975)

Of the 21 names listed above, 10 still represent valid taxa, while the remainder have here been

synonymized. This raises to 46 the number of taxa of sect. *Pachyneurium* at the time this researcher began working with the Araceae (in approximately 1976). Subsequent to 1976, an additional 16 species of sect. *Pachyneurium* have been described. In "The Genus *Anthurium* (Araceae) in Costa Rica," Croat & R. A. Baker (1979) described six additional species: *A. brenesii*, *A. prolatum*, *A. schottianum*, *A. seibertii*, *A. standleyi*, and *A. upalaense*. Two more species were described in preparation for a revision of *Anthurium* for Panama, namely *A. luteynii* and *A. purpureospathum* (Croat, 1981); two species, *A. halmoorei* and *A. salvadorense*, were described in "A Revision of the genus *Anthurium* for Mexico and Middle America" (Croat, 1983) and two more, *A. nervatum* and *A. pseudospectabile*, were described in "A Revision of the *Anthurium* of Panama" (Croat, 1986). In addition, a number of Venezuelan species have been described by Bunting (1986, 1988, 1989) since this project began. These include *A. xanthoneurum* and *A. quanchezii* (1986), *A. vinillense* (1988, along with three others introduced into synonymy), and *A. iramirezae* (1989). Finally, one species, *A. plowmanii*, was described during the preparation of the treatment of the Araceae for the "Flora de Paraguay" (Croat, 1987). The current work includes a total of 114 species, representing 126 taxa, 48 of those being described for the first time. This is 147% more species than were recognized at the outset of the work.

Sectional Relationships Within *Anthurium*

Section *Pachyneurium* is one of 18 sections recognized by Engler (1905). While Schott (1860) recognized 28 groups (and this probably will prove to be closer than Engler to the actual number of needed sections in *Anthurium*), he was dealing with only a small percentage of the species known to Engler. Engler no doubt found it necessary to broaden the concepts of the subgeneric groups in order to include all the new species. In doing so, some groups lost definition. This is particularly true in the case of the species he placed in sections *Belolonchium*, *Urospadix*, *Polyphyllium*, and *Xialophyllium*, all of which (and especially the first) contain what appears to be a wide variety of seemingly unrelated species. A discussion of these groups, their typification, and proposals for some realignment will be the topic of a future paper.

Section *Pachyneurium* is distinct in its ecological requirements and is the most edaphically adapted of all the sections to xeric growing conditions. Because of this, the taxa in the section are most prevalent in areas where there is a pronounced dry season, especially in areas of tropical moist forest. While species in sect. *Pachyneurium* occur in most life zones, most occur in tropical dry, premontane dry, and tropical moist forest. Relatively few species occur in tropical wet, premontane wet, or montane wet forest life zones. No *Pachyneurium* species is known from pluvial tropical forest.

In habit, especially in terms of their short stems, short, densely rooted internodes and mostly erect leaves held in a tight rosette, *Pachyneurium* species resemble most closely species of sect. *Porphyrochitonium*. Indeed, some members of that section, for example *Anthurium hacumense* Engl. (placed in sect. *Pachyneurium* by Engler), are often confused with *Pachyneurium* (Fig. 5). Still, species of *Porphyrochitonium* differ by having dark glandular punctations on one or both leaf surfaces, and in having convolute, not involute, vernation and berries which are often depressed apically with two or more seeds per locule. In addition, sect. *Porphyrochitonium* is ecologically very different, inhabiting some of the wettest life zones such as pluvial rainforest. The Chocó region of Colombia, for example, which is one of the wettest places on earth with more than 500 inches (2,272 mm) of rainfall per year, is the center of diversity for sect. *Porphyrochitonium*. Possibly also a member of sect. *Porphyrochitonium* is *Anthurium hookeri* Kunth, which resembles sect. *Pachyneurium* more than any other non-*Pachyneurium* (Fig. 6). It differs from typical *Porphyrochitonium* in being much larger and in having scalariform secondary lateral veins and perhaps belongs in a section of its own.

Much more easily confused with sect. *Pachyneurium* than sect. *Porphyrochitonium* is a relatively small group of species which also has the "bird's-nest" habit and shares similar oblong to oblanceolate or obovate leaf blades, but without involute vernation (a feature considered an absolute requirement regardless of habit or blade shape). Typical of this group is *A. michelii* Guill. (Fig. 3), once considered to be a member of *Pachyneurium* (Croat, 1983). These species, with epunctate, oblanceolate to oblong-elliptic blades and generally short stems with short internodes are mostly small plants not easily confused with typical *Pachyneurium* species, but some of the larger ones, such as *A. michelii*, are in fact easily confused with *Pachyneurium*. This group of plants has not been placed with certainty in any group, though it is tentatively placed in a new section including *A. decurrens* Poeppig, placed by Schott (1860) in his grex *Oxycarpium*. Since only three species, *A. decurrens*

Poeppig, *A. oxycarpum* Poeppig, and *A. consobrinum* Schott were included in Schott's grex *Oxycarpium*, and since the two latter species are now placed in sect. *Pachyneurium* (along with the epithet sect. *Oxycarpium*, which is now synonymous with sect. *Pachyneurium*) only *A. decurrens* remains. The name for this new section will be proposed in a future paper. This new section is the only section (other than sect. *Urospadix*) with short internodes and elongate, epunctate leaf blades with convolute vernation. Section *Urospadix* is, I believe, distinct from the latter section based on generally closer, more uniform primary lateral veins and its more restricted geographical distribution, mostly in southeastern Brazil.

Section *Urospadix* (Fig. 4) is the next most likely group to be confused with *Pachyneurium*. These two are probably not closely related owing to their lack of involute vernation (although one probable species of sect. *Urospadix* has hybridized with a *Pachyneurium*—see section on breeding behavior). Given that this character state, a conservative ontogenetic feature, is present only in sect. *Pachyneurium* and in only one other genus in the family, *Lagenandra*, it seems apparent that sect. *Pachyneurium* has no close relatives. Nevertheless, sect. *Urospadix* has many features in common with *Pachyneurium*, especially the short stems, close internodes, frequently rosulate habit and the presence of elongate, often short-petiolate leaf blades. In gross morphology they differ from members of series *Pachyneurium* in their generally closely spaced and moderately obscure primary lateral veins. Some members of sect. *Urospadix* are very similar to members of series *Multinervia*, a group mostly restricted to the Ecuadorian Andes. From species of series *Multinervia* they differ principally in having supervolute vernation, and in being geographically isolated in the geologically more ancient parts of eastern South America, namely Brazil. Section *Urospadix* ranges principally from the state of Bahia to São Paulo with at least two outlying species (tentatively placed in this section), one in the Venezuelan highlands (*A. yutajense* Bunting) and one from the Cordillera de la Costa (*A. lilacinum* Bunting).

Some other groups of *Anthurium*, especially species currently placed in sect. *Belolonchium* in Central America and in the West Indies, have species that are similar to those few species of *Pachyneurium* with cordate or subcordate blades, e.g., *A. venosum*, *A. ranchoanum*, *A. schottianum*, *A. standleyi*, *A. colonicum*, and *A. cotobrusii*. It is believed that this latter group of *Pachyneurium* has independently evolved the cordate condition rather than having independently acquired involute vernation. The reasoning here is that leaf vernation is a conservative ontogenetic character whereas leaf blade shape in the genus is a highly plastic one. Indeed, leaf shape may be highly variable even on individual plants (see section on leaf blades under Morphology).

The Central American species of *Anthurium* are now well known, and all suspected species have been screened for the presence or absence of involute vernation. Despite the fact that the endemic South American *Pachyneurium* species are less well known, many cordate South American species have been studied in cultivation, and no *Pachyneurium* species have been found among them. Thus the phenomenon of subcordate- or cordate-leaved *Pachyneurium* seems to be largely a Central American and West Indian one. It is in these regions where some cordate *Anthurium* species with short stems, short internodes and blades with free-ending veins (a relatively common feature in many cordate-leaved *Anthurium*) might be confused with sect. *Pachyneurium*. Engler placed a number of these species in his sect. *Pachyneurium* (Appendix 2). These included *A. longispathum* Carrière (= *A. grandifolium*), *A. grandifolium* (Jacq.) Kunth, *A. boucheanum* K. Koch (= *A. cartilagineum* (Desf.) Kunth), *A. liebmannii* Schott (= *A. umbrosum* Liebm.), *A. umbrosum* Liebm., *A. cordatum* (Willd.) G. Don, *A. andicola* Liebm., *A. cartilagineum* (Desf.) Kunth, *A. brownii* Masters, *A. appunianum* Schott (= *A. cartilagineum*), and *A. seleri* Engl. Except for *A. seleri*, most have many of the general features of sect. *Pachyneurium* and are in many ways similar to Central American and West Indies cordate-leaved species of *Pachyneurium*, except that they lack involute vernation. Thus, it is not surprising that Engler, apparently unaware of the important character of involute vs. supervolute vernation, placed these species in sect. *Pachyneurium*. On the other hand, using general characters such as leaf shape, short stems, and short internodes alone, many additional species from the West Indies, Central and South America might well have been placed by him in sect. *Pachyneurium*.

In general, South American species are either not subcordate-leaved, or their blades are decidedly elongate with merely the bases being subcordate (e.g., *A. fendleri*).

The remaining sections of *Anthurium* are not at all similar to members of *Pachyneurium* and need not be discussed.

Morphology of Vegetative Structures

growth patterns

The shoot organization of *Anthurium* sect. *Pachyneurium* has been characterized by Ray (1986, 1987, 1988). Though appearing unbranched, the stems of most anthuriums are in fact highly branched with a growth pattern described as triphyllous sympodial (Ray, 1988). Each article (or segment) of the shoot includes a sylleptic prophyll (P) and mesophyll (E) (both of which are cataphylls) as well as a sympodial leaf (S) (a foliage leaf) and a solitary, terminal inflorescence (I). Vegetative buds are formed only on the sympodial segment and on the peduncle base (which is axillary to the mesophyll and the foliage leaf). This growth pattern can be summarized as follows (after Ray, loc. cit.).

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{P − E − S − I}

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Studies by Tom Ray (pers. comm.) have defined the shoot organizations and growth patterns. In this regard sect. *Pachyneurium* is identical to that of all species of *Anthurium* with the exception of sect. *Polyphyllium*. It is the sylleptic prophyll which is termed the cataphyll throughout this work and previous works by this author on *Anthurium* (Croat, 1983, 1986). The stem thus consists of a series of units (articles), each of which comprises a branch with a single foliage leaf subtending (eventually) a continuation shoot and a terminal inflorescence.

stems

The stems of *Anthurium* sect. *Pachyneurium* are characterized primarily by being generally short and densely rooted. While most members of other sections of *Anthurium* (excluding *Xialophyllium* and *Tetraspermium*) have short to moderately short internodes as well, few sections ever have species with such extremely short internodes. Typically, those of sect. *Pachyneurium* are several times broader than long. Moreover, the caudex differs in being much more densely rooted than in other sections. Depending on the size of the stem and especially the size of the petiole bases, the stem diameter is highly irregular from node to node with the petiole bases conspicuously swollen while the very narrow intervening areas between them are devoted entirely to cataphylls and roots. The abscission scar of the petiole is generally broader than high (i.e., broadest laterally, perpendicular to the axis), though the shapes of the scars are usually not as variable throughout the section as is the range of variation of petiole cross sections. Petiole abscission scars are generally rounded abaxially and broadly rounded adaxially. The abscission scar is typically inclined inward to the axis at an angle of 110–140° from the axis of the stem. Unlike many *Anthurium* species with longer internodes, *Pachyneurium* has leaf scars that are usually not easily visible but remain obscured by the persistent cataphyll fibers and roots (Fig. 7).

The stems of *Pachyneurium* are generally short, usually less than 20 cm long, and rarely more than 30 cm long except in very large old plants. Stem diameter varies from as little as 1.5 cm in some of the smaller species to about 7 cm diam. in the larger species, generally averaging 3–4 cm diam. Stem diameter is in part also a matter of age, but mostly increases only slightly during the life of the plant.

Usually the oldest part of the stem rots away except for that portion contained in the living root mass. Older parts of the stem are frequently attacked by root borers, which enter through the softer central portion of the stem and bore up into the younger portions. However, perhaps because of the seasonally dry habitats and the generally massive root ball, which provides protection to the stem, sect. *Pachyneurium* exhibits fewer cases of infestation by root borers than perhaps any other section of *Anthurium*.

Only rarely do *Pachyneurium* species have noticeably elongate internodes. Some species, such as *A. consobrinum*, tend to grow rapidly when young, producing internodes to several centimeters long, before reverting to a slower growth with short, broad internodes. Some species may revert to a growth pattern with slightly longer internodes when disturbed or dislodged from their positions in trees, especially when they land on their sides or land upside down. This reversion to longer internodes, so common in other genera and even in other sections of *Anthurium*, is not common in *Pachyneurium*, and even when reversion to production of longer internodes does occur, the duration of long internode production is always very brief.

Of the two series of *Pachyneurium*, series *Mul-*

tinervia has a stronger tendency to produce longer internodes. This no doubt owes to their generally more mesic habitats at higher elevations, where the closer, more compact stems have less advantage (and perhaps some disadvantage since the more typical plants in series *Pachyneurium* would probably become waterlogged and rot in such cooler, wetter environments).

Pachyneurium stems are tough and moderately inflexible, perhaps owing to the presence of numerous coarse fibers. Only the central or older parts of the stem are soft, offering one of the few avenues for predation (the other being through the soft area of the abscission scar where the old peduncles have rotted away).

Pachyneurium stems are typically erect, whether habit is terrestrial or epiphytic. In a few rare cases stems may be repent, e.g., in *A. lindmanianum*. This is presumably an ecological adaptation, providing the plant with a better means of survival. *Anthurium lindmanianum* usually occurs in seasonally dry areas as a terrestrial plant along the edges of watercourses. In cultivation, the species will grow well in a standing pool of water on rocks or bricks above the water level. Its roots extend into the water and the typical rosulate habit is still maintained because the petioles are turned sharply at right angles to the stem and are held erect.

Despite the obvious ecological advantage of repent stems in drier areas, this habit has not evolved frequently in *Pachyneurium*. More commonly, even in extremely dry habitats, the stem and leaves are stiffly erect.

Stems may be horizontal to almost pendent in *A. pseudospectabile*, which grows suspended from a few roots. Potted plants of this species may grow in a curve until the apex is again directed more or less downward.

ROOTS

Perhaps more than any other section, *Pachyneurium* shows considerable variability in root disposition. Depending on the habitat and the species, some species, especially short-petiolate ones, may produce most of their roots so that they are directed upward or downward or spreading. Typically, in epiphytic species in mesic habitats that experience a pronounced dry season, at least the uppermost roots are directed upward and are frequently narrowed and pointed at the ends as well (Fig. 8). This provides a clear advantage for collecting falling debris and precipitation around the roots (Figs. 7, 13). These uppermost roots frequently even grow into the basket often formed by the rosulate habit and the short-petiolate leaves (Figs. 7, 8, 14). The uppermost roots are the most active in terms of growth, and generally act as feeder roots.

Even in such situations, still other roots, usually those further down on the stem, act more for anchorage and support. These are also generally longer, stouter, and less well ordered, being instead more frequently intertwined. They are nevertheless equally capable of entrapping debris and are, at least near the periphery of the living root mass, debris-infested. Because long-petiolate species are less likely to be efficient at catching debris, they are more likely to have their roots directed downward rather than upward (Fig. 9).

The root masses of most species are extremely compact, the roots generally being completely contiguous with one another near the surface of the stem in most species of series *Pachyneurium* (Fig. 10). Some species, especially many members of series *Multinervia*, have less densely aggregated roots. This compact nature of the root system not only enables the plant to adapt well to dry conditions, allowing it to absorb quickly virtually all of the rainwater that passes through in brief rain showers, but also is effective in keeping phytophagous insects, especially root borers, away from the stem.

Other *Pachyneurium* species, especially the terrestrial ones, frequently have their roots directed downward along the stem and into the ground. These species, despite the fact that they too often have the typical rosulate habit with short stems, are frequently growing under conditions where they are less likely to accumulate debris from falling leaves, etc., and often grow out in the open or under low forest, which does not yield such high quantities of debris. Some terrestrial species, such as *A. atropurpureum* var. *atropurpureum*, *A. pachylaminum*, or *A. bonplandii*, often occur on white sand soils, which are notoriously poor in nutrients, and are either found growing in open areas or growing beneath typically evergreen trees on white sand soils. In such situations, roots directed into the soil appear to be an adaptation to take better advantage of nutrients present in the soil, which might not be available from accumulated debris. On some species, e.g., *A. linguifolium*, from a very arid area, the uppermost feeder roots are much reduced and directed upward rather than downard.

The roots themselves, usually 3–8 mm diam., are initially covered with a dense layer of root hairs, so dense as to appear as a smooth and continuous layer. Artificial drying of the stems, which

causes a shrinkage of the roots and root hairs, reveals their true nature, wherein the roots generally appear woolly-pubescent. At least one exception to the typically smooth roots on fresh plants is seen in *A. johnsoniae*, which has fresh roots with a somewhat irregular warty surface.

In addition to obvious functional differences, the roots have taxonomic importance, especially the color, thickness, degree of spreading, and length of the uppermost feeding roots.

CATAPHYLLS

The cataphyll is a modified leaf that protects the newly emerging leaf. It is termed the sylleptic prophyll by Ray (1986, 1987, 1988). Once the leaf emerges, the cataphyll has no functional significance in remaining photosynthetic (for ecological significance see below) and promptly dries up. Though the cataphylls of *Anthurium* do not contribute as many useful characters as do those of *Philodendron*, the cataphyll in sect. *Pachyneurium* is more diverse than in any other section of *Anthurium*. There are two basic types of cataphylls, with one type subdivided:

(1) cucullate (hood-shaped) (Figs. 15, 46)
(2) narrowly triangular or lanceolate
  (a) straight (Fig. 11)
  (b) hook-shaped (Fig. 16).

The former type is rare, known for certain only in *A. salviniae* and *A. barclayanum*. It is interesting to note that the cucullate cataphylls (and sometimes also hook-shaped cataphylls, e.g., *A. loretense*) also have leaves which are circinate in bud in addition to having involute vernation (Fig. 17). Upon unrolling, the young leaf first unrolls lengthwise, then unrolls toward both margins in the usual manner of sect. *Pachyneurium*.

The second cataphyll type, narrowly triangular or lanceolate, is overwhelmingly more common, and most of these are straight and erect. In South America some species have narrowly triangular cataphylls that are hooked (the phenomenon is absent among Central American species). Plants with typically hook-shaped cataphylls also have sharply D-shaped petioles in cross section (Fig. 16). Blades emerge in the same fashion in both types of narrowly triangular cataphylls, but the hook-shaped type are usually smaller than the straight ones and thus the emerging leaf is usually smaller before expansion. Nevertheless, the overall size of the fully expanded leaf blade does not seem to correlate with the size of the newly emergent but unfolded leaf blade, since some species with hook-shaped cataphylls have among the largest leaves in the section, e.g., *A. loretense*.

Fresh cataphylls of *Anthurium* are uniformly green (unlike *Philodendron*, where they may be colorful), and except for length and shape they are monotonously similar. Moreover, the cataphylls dry promptly after the emergence of each new leaf and thus usually no more than one fresh cataphyll is visible. The old, dried cataphylls are more significant taxonomically, perhaps more characteristic than those of other sections of the genus. Although some species, e.g., *A. eximium*, *A. luteynii*, *A. upalaense*, and *A. willifordii* have cataphylls that dry persistent and intact, most persist in a weathered state (Fig. 12). The degree to which weathering takes place varies substantially. While some weather to disorganized and inconspicuous fibers that are mostly obscured by the roots and petiole bases (Fig. 14), other species, especially those with longer cataphylls, dry with their fibers in an organized or semiorganized intact fashion, e.g., *A. luteynii* (Fig. 18) and *A. pendulifolium* (Fig. 9); others dry intact, and then quickly weather to fibers (Fig. 19). In addition to the length of the cataphyll, which may vary from 3 to 40 cm, there are differences of color and thickness, which are taxonomically significant. Unfortunately, like many other characters in *Pachyneurium*, these differences are difficult to quantify as key characters.

Though of minor importance taxonomically, cataphylls have an important function ecologically. They generally weather into fibers which, in conjunction with the roots, aid in entrapping debris.

LEAVES

Petioles. The petioles of sect. *Pachyneurium* are typically much shorter than the blades and this, coupled with the short internodes, provides the basic ingredient for the rosulate habit and "bird's-nest" appearance. Some species of *Pachyneurium*, even the more typical members of series *Pachyneurium*, may have long petioles, but they are less effective as debris catchers and even tend to have leaves spreading laterally, e.g., *A. llewelynii*, or pendent, e.g., *A. pendulifolium*, *A. pseudospectabile*, and *A. spectabile*.

Petiole cross-sectional shapes of sect. *Pachyneurium* are diverse, perhaps more so than in any other section of *Anthurium*. *Pachyneurium* species have at least some of the cross-sectional shapes in each category from A through E (Fig. 21). Cross-sectional shapes in *Pachyneurium* are mostly "D-shaped" (category B), "markedly angular" (D) and "markedly ribbed adaxially" (E) with fewer species

having petiole cross sections in category A, "terete." The U-shaped cross-sectional shape is rare in sect. *Pachyneurium*. Many species of *Pachyneurium* have C-shaped petioles (A 6–8), and petiole shapes that are more or less trapezoidal to D-shaped with prominent abaxial ribs are especially common (E 1–3).

The petiole base is usually briefly sheathed (Figs. 14, 16) and encircles the inflorescence (the latter may abort). The sheath is usually inconspicuous and short, only rarely extending up to as much as 8 cm long. In most cases the sheath is restricted to a very small percentage of the total length of the petiole but may, for example in *A. consobrinum*, *A. fatoense*, and *A. harlingianum*, have sheaths that extend almost to the base of the blade. The petiole in all *Pachyneurium* species terminates in a conspicuously swollen geniculum, which facilitates leaf blade orientation.

Blades. Vernation—The nature of the developing blade is highly significant taxonomically, especially at the sectional level in the case of sect. *Pachyneurium*. *Anthurium* sect. *Pachyneurium* is the only section of *Anthurium* known to have involute vernation of the developing leaf blades. Indeed, only one other genus in the Araceae, *Lagenandra* from the Old World Tropics, has involute vernation. With involute vernation the developing leaf (in bud) has both margins of the blade rolled inward toward the midrib (Fig. 1), whereas supervolute vernation, the common type of vernation for *Anthurium*, has one margin rolled inwardly to the midrib and the other rolled around the coiled up inner blade margin, as well as the midrib (Fig. 2).

Although the presence of involute vernation is consistent on adult plants, juvenile plants of *Pachyneurium* species may have supervolute vernation or a transitional stage of development where only a part of a leaf blade (usually the widest part) has involute vernation. Richard Sheffer (pers. comm.) reports observing a series of leaves from a single plant where the vernation of successive blades progresses gradually from wholly supervolute blades when juvenile, to partially involute blades to wholly involute blades in adult plants. In series *Multinervia*, which has in general more slender blades, the tip of the blade is frequently supervolute while the remainder of the blade has typical involute vernation. This failure of the apical portion to be involute is probably due to the difficulty in rolling up an increasingly narrower section of leaf tissue.

General features—Although species in sect. *Pachyneurium* typically have thick, oblanceolate to obovate leaf blades with short petioles, the group is actually quite variable in blade shape with blades ranging from linear-oblong to ovate-triangular to ovate, with bases acute to subcordate or cordate. The less typical species, such as *A. schottianum*, *A. standleyi*, and *A. watermaliense*, have moderately thin blades with distinct posterior lobes. Typically, blades are more or less elongate, broadest at or above the middle of the blade and gradually tapered to the base, but frequently the blade ends abruptly and is often rounded at the base or even subcordate (e.g., *A. fendleri*) despite its generally oblanceolate or obovate overall shape. Leaf blades may be quite variable at the base, even on the same plant varying from shallowly cordate to acute (Fig. 20).

While the blade of most *Pachneurium* species extends to the base of the midrib and ends immediately above the geniculum of the petiole, some species have a large section of the midrib completely naked, so that it appears to be a part of the petiole proper. This is perhaps most extreme in *A. oerstedianum*, but other species, such as *A. guanchezii*, *A. pranceanum*, and *A. remotigeniculatum*, also display this feature. While this feature exhibits some taxonomic value, it does not always represent a character warranting specific recognition. This is true, for example, in *A. bonplandii* subsp. *bonplandii*, which sometimes has the geniculum appearing remote for a few centimeters, but does not otherwise appear to be different from other plants of the taxon (see *Schultes & Cabrera 14083*). Venation is relatively uniform considering the wide range of blade shapes. Usually the major veins are prominently raised on both surfaces, with the midrib varying from slightly convex to angular above and typically more prominently convex below. Frequently, if the midrib is angular above, this is owing to a continuation of a medial rib on the adaxial surface of the petiole, but more commonly the midrib is flat at the very base on the adaxial surface. From this point the midrib may become progressively more raised and more acute toward the apex, the most acute portion being in the distal 2/3 of the blade. From this point the midrib commonly becomes diminished and is usually even weakly sunken at the very tip. This is generally true also when the midrib on the adaxial surface is merely rounded or obtuse rather than acutely raised.

On the lower surface, the midrib may be convex or angular, but when it is angular it is usually due to an extention of the ribs onto the petiole. In this case, the ribbing on the abaxial surface of the petiole is often present on the geniculum as well, e.g., in *A. luteynii*.

For typical members of sect. *Pachyneurium*

(always true for series *Pachyneurium*), the primary lateral veins are prominently raised on both surfaces (hence the sectional name), most commonly departing from the midrib at 30–55° in the middle of the blade and sometimes at broader angles, approaching 90° near the base of the blade. Rarely, as in *A. reflexinervium*, *A. paraguayense* var. *coroicoanum* and *A. latissimum*, the veins may arise at an angle of 90° or more near the base of the blade and the primary lateral veins may actually be retrorse in such cases.

Blades with rounded, cordate or subcordate bases tend to have an aggregation of veins at or very near the base of the blade. For those species with rounded or subcordate bases, all but the lowermost are considered primary lateral veins, whereas those species with cordate bases generally have a series of basal veins (as defined in Croat & Bunting, 1979). These basal veins in all species with well developed posterior lobes are generally directed downward into the lobes and may be in part united into a collective vein (Croat & Bunting, 1979).

Pachyneurium species rarely have interprimary veins or secondary veins (i.e., major branches off of the primary lateral veins), both of which are often well developed in other sections of *Anthurium*. Tertiary veins on the other hand are usually well developed, and reticulate veins are often well developed and conspicuous at least after drying. In some species, most notably *A. crenatum*, the reticulate veins are quite conspicuous even on fresh leaves. The largest tertiary veins are generally very conspicuous in most species and are generally weakly raised on the lower surface and moderately obscure on the upper surface. However, some species, such as *A. jenmanii*, *A. bonplandii*, and *A. atropurpureum*, have many of the tertiary veins sunken or etched into the upper surface on fresh leaves.

Blade margins of most *Pachyneurium* are entire (though somewhat sinuate in *A. barclayanum* and *A. paraguayense*) and may be flat to markedly undulate, such as in *A. affine*. Typically, blades are cuneate (gradually and evenly narrowed toward the base so that the margin in the lower part of the blade is straight). However, in some cases, e.g., *A. latissimum*, *A. palenquense*, *A. remotigeniculatum*, the blades are attenuate with concave basal margins.

Features on blade surfaces are noticeably absent in most species, though many of the species in the Amazon basin, especially those occurring in areas where white sand soils predominate, frequently exhibit raised pustules. Some species, notably *A. bonplandii*, have weakly raised plate-shaped, glandlike structures which may be darker than the surface and visible to the naked eye. These are especially conspicuous on *A. bonplandii* subsp. *guayanum* and *A. xanthoneurum*. Rarely, blades may be glaucous on the lower surface as is sometimes the case in *A. caucavallense* and *A. glaucospadix*, but even in these species not all plants possess glaucous blades.

Morphology of Reproductive Structures

INFLORESCENCES

As in other *Anthurium* sections, members of sect. *Pachyneurium* have a single inflorescence per leaf axil arising from the sheath. Commonly, the inflorescence emerges fairly promptly from the leaf axil, requiring one to six weeks to fully emerge. Although every leaf axil has the potential to produce an inflorescence, the inflorescence may abort, and usually does so before the plant reaches a certain age. Usually, the inflorescences emerge one at a time from the axils of the uppermost leaves (but rarely from the youngest, i.e., most recently emerged leaf). In this manner a plant may have several inflorescences present, but rarely as many as four per plant. Usually a plant has one or two inflorescences, each in a different stage of development. The rate of the emergence of the inflorescences usually precludes the possibility of self-pollination because they do not reach anthesis at the same time (see section on Flowering Behavior). In unusual cases, the inflorescences may emerge from several leaf axils within a short span of time, e.g., in *A. schottianum*. In this case the inflorescences are still not of the same age, but they are more nearly alike in age than is normally the case. This also has an important bearing on the phenology, since this species tends to flower in short, brief bursts rather than periodically throughout the year (see section on Phenology).

Peduncles. Peduncle length in *Pachyneurium* is highly variable even within the same species and at different phases of an individual plant's life. Nevertheless, the petiole–peduncle length ratios are often highly significant taxonomically, at least at anthesis. The peduncle is generally terete and green, or occasionally with an acute angle on one side of the peduncle which extends along much of its length, or rarely with several ribs around the circumference of the peduncle. Most species have peduncles that vary from somewhat longer to several times longer than the petioles, and only rarely is the peduncle shorter than the petioles (e.g., *A. curtispadix*, *A. plowmanii*, and sometimes *A. ernestii* and *A. purpureospathum*). Typically, the peduncle is moderately stiff and is held erect or

semierect at least during anthesis. After anthesis, the peduncle either begins to turn yellow and shrivel, in the event that pollination has not occurred, or it becomes heavier with the development of fruits and the weight of the resulting infructescence causes the peduncle to bend outward or even downward.

A few species, such as *A. cataniapoense*, *A. salviniae*, *A. pendulifolium*, and often *A. solitarium*, have long, slender peduncles with the inflorescences pendent at anthesis. Regardless of whether the peduncle is thick, stiff, and erect or slender and pendent, it becomes thicker in the fruiting stage to compensate for the added weight of the berries. The net weight of the inflorescences may increase during maturation by a factor of 20 or more. Because of the heavy weight of the infructescence, very few species, even those with erect inflorescences, bear their fruits in an erect position. Among those that do are: *A. cubense*, *A. plowmanii*, *A. purpureospathum*, and *A. superbum*, all of which have very short peduncles.

Spathes. Although sect. *Pachyneurium* has spathes that are not so typically colorful or as taxonomically useful as in other sections of *Anthurium*, especially sect. *Calomystrium*, the spathe still carries considerable taxonomic weight in the recognition of species. The typical spathe of *Anthurium* sect. *Pachyneurium* is oblong-lanceolate, acuminate at the apex and with the distal margins often slightly inrolled. Typically, the spathe is inserted at about a 45° angle on the peduncle. The base is generally acute to attenuate and is often decurrent onto the peduncle for a short distance. Usually somewhat coriaceous or subcoriaceous, the spathe completely envelops the spadix only when the latter is very young. The spathe is generally loosened and free from the spadix before the pistils of the flowers are visible. Ordinarily, the spathe is initially erect for a time after it opens, the natural result of its erect position while in bud, but in most cases the spathe soon spreads and may ultimately be erect-spreading or spreading, or it may become spreading-reflexed to reflexed and even caducous (e.g., *A. fendleri*). These spathe positions are not always taxonomically significant, and a single spathe may go through a series of positions throughout the course of its development. Still, many species have spathes that are characteristically positioned in a particular manner, usually comprising no more than two of the above positions for one taxon. The spathes of *A. bradeanum*, *A. sarukhanianum*, and *A. salvadorense* remain erect and may enshroud the spadix in the two latter species.

The spathe is usually curved along most of its length after spreading so that, strictly speaking, no directly measureable angle is formed with respect to the peduncle. In addition, the spathe may be variously undulate, inrolled, or twisted. In some cases this feature may be extreme, e.g., in *A. colonicum*, *A. pseudospectabile*, and *A. spectabile*, where the spathe becomes very much contorted.

While the spathes of *Pachyneurium* are typically thick and persistent, some species, mentioned above, have thin spathes which begin withering almost from the moment they open, and generally wither off and fall free in time. Even in some species with typically thicker spathes, such as *A. jenmanii*, the spathe withers, or at least yellows, shortly after anthesis. In these cases the spathe, though withered, usually does not fall free, but remains on the spadix in its withered state.

Spathes are generally about as long as the spadix but may be substantially shorter at anthesis or even longer than the spadix as in the case of *A. eximium*, *A. galactospadix*, and *A. spathiphyllum*. While the absolute lengths of the spathe and spadix are variable throughout the course of a plant's development and are thus usually not so valuable as key characters, the relative length of the spathe in relation to the length of the spadix may provide a useful character, especially when studied at anthesis. The proportional differences in the size of both the spathe and spadix during their development need not remain constant. For example, the spathe does not greatly elongate after anthesis for some species, such as *A. fendleri*, whereas the spathe of *A. salviniae* increases in length after anthesis.

Spadices. The spadix shape of *Anthurium* can vary from long-tapered to oblong (Fig. 59) or spindle-shaped or even obovoid or subglobose. The spadix of most *Pachyneurium* species is typically short-tapered (Fig. 232) or long-tapered (Fig. 44). A few species, such as *A. cubense*, *A. superbum*, *A. bradeanum*, *A. affine*, and *A. spathiphyllum*, have spadices that are oblong-cylindric or clavate, while *A. sarukhanianum* has a narrowly obovoid spadix (Fig. 277). Spadix color, though variable, is not very useful for *Pachyneurium* because so many species have spadices that are green or purplish, with only a relative few being red (sometimes in *A. ernestii*), white (*A. superbum*), yellow, or other colors. In addition, spadices of some species (e.g., *A. barclayanum*) may vary from green to purplish. *Anthurium ernestii* is markedly variable according to herbarium labels, with spadices at least varying from pinkish to magenta to purple, dark

red, or green. Overall spadix size in *Pachyneurium* is variable and depends on the size and age of the plant and its condition. As indicated above under "Peduncle," the relative length of the spadix compared to the peduncle may be important taxonomically. However, even this character is sometimes highly variable and may vary depending on the age and health of the plant.

Flowers are arranged in close spirals (Croat, 1980) with mostly more than five flowers visible per spiral from any angle. The number of flowers visible per spiral, though somewhat variable from spadix to spadix for any species, may also be taxonomically significant, with the number ranging from as few as 3 or 4 flowers visible per spiral for *A. vaupesianum* and *A. uleanum* var. *nanayense* to as high as 28 flowers visible per spiral for *A. galactospadix*, and 24 for *A. superbum*. Descriptions of the number of flowers per spiral refer always to the number of flowers visible from any angle rather than the number actually needed to make a complete spiral (the reason being that the reader could not easily interpret the number of flowers on a herbarium sheet).

As is true of all *Anthurium* species (Croat, loc. cit.), *Pachyneurium* flowers have four tepals, which are mostly hidden from view without dissection. They are arranged symmetrically on four sides of the pistil. Tepals are narrow, thin, and generally colorless except at the apex. Tepals are markedly cucullate at the apex and mostly cover the apex of the pistil. The apical portion of each tepal is more or less 3-sided, with the inner margin (that portion directed inward toward the stigma) thin and sometimes turned up against the pistil, especially when the pistil is exserted, as in *A. consobrinum*. "Tepal shape" when referred to throughout this work refers only to the apical, visible portion of the tepals. In the same way "flower shape" refers only to the apical portion of the flower. Flower "length" refers to the width of the apical portion of the flower in the longitudinal dimension of the spadix, while flower "width" refers to the width of the apical portion of the flower in the lateral dimension (i.e., perpendicular to the axis of the spadix). The actual length of the tepals, including the hidden portion which extends into the axis of the spadix, is never measured.

Tepal shape may be important taxonomically. Most are basically triangular, with the inner margin almost straight to rounded to broadly rounded. The outer margin, though commonly two-sided, is more variable. Some species, e.g., *A. barclayanum*, *A. curtispadix*, and *A. glaucospadix*, may have tepals which have the outer margin 3- or 4-sided. In the latter case the tepal may be referred to as "shield-shaped."

Androecium. Like all *Anthurium*, sect. *Pachyneurium* has four stamens, each of which is affixed at the base of a tepal. Stamens are tightly compressed between the tepals and the pistil and are not visible without dissection prior to anthesis. The filament is slender (typically much narrower than the hidden portion of the tepal), conspicously flattened, and generally colorless and translucent or sometimes whitish. Fresh filaments are usually somewhat succulent with a thin epidermis. Shortly before maturity of an individual stamen, the anther is pushed out from between the tepal and the pistil by elongation of the filament. Once exposed, both thecae of the anthers promptly open by longitudinal slits. Dehiscence is extrorse. Thecae are generally more or less oblong or ovoid, and unlike some sections e.g., *Porphyrochitonium*, are generally only slightly divaricate (e.g., with the two thecae diverging away from one another toward the base). For further details of stamens see section on Flowering Behavior.

Gynoecium. Typical of other sections of *Anthurium*, the pistils of sect. *Pachyneurium* are bilocular, more or less oblong-ovoid, and are tightly compressed in between the four tepals. A well-defined style is always lacking. The pistils are visible only at the apex and sometimes are almost completely covered by the tepals. Generally, only the stigma is visible. Each locule contains a single ovule with axil placentation. For additional details of the gynoecium see section on Seeds.

Stigmas consist of an elongate slit (Croat, loc. cit.). Generally those of sect. *Pachyneurium* have the stigmatic hairs contained within the slit, densely covering both sides of the inner surface. Occasionally, e.g., *A. palenquense*, the stigmatic hairs may be long-exserted, forming a brushlike stigma. Stigmatic fluid is produced by the stigmas and generally accumulates to form conspicuous droplets. For additional details, see section on Flowering Behavior.

FLOWERING BEHAVIOR

Long-tapered spadices generally have flowers developing from the base of the inflorescence and progressing toward the apex. Those with oblong or narrowly obovoid spadices generally have the first flowers to reach anthesis at the middle or lower one-third of the inflorescence with development progressing toward both ends. For a review of flowering behavior of *Anthurium* see Croat (1980).

All other features of flowering behavior are identical to those described in that paper. Typically, *Pachyneurium* species have spadices at anthesis for long periods. While most species have spadices in anthesis for about a week, some, such as *A. luteynii*, may have spadices in anthesis for several weeks. As in other species of *Anthurium*, flowers are usually markedly protogynous, with the pistillate phase clearly separated from the staminate phase. During the pistillate phase most species in sect. *Pachyneurium* produce nectar droplets on the stigmas. Some species, such as *A. concolor*, may also produce droplets of nectar on the tepals as well. In natural situations these droplets are rarely allowed to accumulate, apparently being removed by pollinators, but in cultivation the droplets may accumulate to such an extent in some species, e.g., *A. upalaense*, *A. validifolium*, and especially *A. lutyenii*, that the nectar drips off the spadix (Fig. 332).

As in other species of *Anthurium*, the staminal development of *Pachyneurium* generally begins with the lateral stamens (Croat, 1980) followed by the alternate pair of stamens with the anterior stamen (referred to throughout this paper as the third stamen) developing before the posterior stamen (referred to throughout this paper as the fourth stamen). In most species of *Pachyneurium*, lateral stamens emerge well ahead of the first alternate stamen, varying from about 3 to 20 spirals ahead of the third stamen (usually the anterior stamen), and the first alternate stamen usually also emerges several spirals ahead of the fourth stamen. Thus, the available fresh pollen is commonly scattered over ⅓ or more of the spadix. When the stamens first emerge, the anther is frequently slightly exserted on a fleshy, thickened filament and is frequently colored. Anthers usually open promptly after emerging from beneath the tepals. Most frequently the pollen color is yellow, orange, or purplish, but is often white. The exserted anther lasts generally less than one day, and the anther is then generally retracted so that it is positioned at or near the level of the tepal (Croat, 1980). The retraction is caused by the loss of water in the thin filaments and the resulting shrinkage. Usually by the end of the first day of emergence of the stamens and always by the next day, the color of the pollen and generally that of the anther has faded (probably due to oxidation) and usually turns white. Some species, especially certain members of series *Multinervia* (e.g., *A. acutissimum*, *A. obscurinervium*, and *A. oxyphyllum*) have stamens that are prominently long-exserted and remain exserted after anthesis.

The fact that pollen has faded in color does not necessarily mean that it is not viable, but fresh pollen is most effective in pollination.

Generally, individual flowers of *Pachyneurium* species are so markedly protogynous that stigmatic droplets have dried up on all flowers by the time the stamens emerge on the lowermost flowers; however, in some cases the stigmatic droplets are present on the uppermost flowers of the spadix, and at the same time the stamens are beginning to emerge on the lowermost flowers of the spadix, thus geitongamy is possible. In fact, it is common practice for plant breeders to manipulate the spadix of a single inflorescence to attempt self-pollination when no other pollen is available. While not always successful, this method will sometimes work on some species.

Morphology of Fruiting Structures

Infructescences

The fruiting spadix of most species of sect. *Pachyneurium* is much expanded in size, the extra girth coming from both an expansion of the pithy axis of the spadix and a general increase in the length of the tepals. The expansion accommodates the greatly expanded size of the developing berry.

Berries. In most *Pachyneurium* species the berry begins to emerge above the tepals and becomes colored well in advance of its actual maturation, i.e., before the seeds are matured sufficiently to germinate. Alternatively, the enclosed seeds usually are capable of germination somewhat before the berry becomes fleshy, loose, and obviously mature. Berries are also capable of maturing to some extent even on severed inflorescences. This is important when collecting seeds before the berries are fully mature. The berries of the mature infructescence generally emerge in sect. *Pachyneurium* in a scattered fashion over a relatively long period of time, but some species, such as *A. spathiphyllum* and *A. consobrinum*, have fruits that emerge more nearly simultaneously. Typically, the berries are weakly exserted and do not fall free for display.

Berry shape is typically obovoid to obovoid-ellipsoid and generally rounded but sometimes acute to narrowly acute at the apex. Berry shape may be variable even within a single population, e.g., in *A. schlechtendalii*, where berries may be acute to rounded at the apex.

Berry color. Berries of sect. *Pachyneurium* are typically concolorous and are summarized in Tables 1–3. Exceptions, with bicolored berries, include:

(1) *Anthurium consobrinum*, with white fruits and red to purple apiculate tips; (2) *A. superbum*, with fruits colored lavender at the base and white at the tip; and (3) *A. pendulifolium* with fruits colored purplish lavender to reddish purple at base and white at the tip.

In general, fruit color (yellow, orange, red, or purple) remains distinct and permanent throughout their maturation. The purple-fruited species, however, are an exception and are much more variable in color during development. An example is *A. pendulifolium*, where pure lavender to reddish violet berries may become almost completely white at maturity. Included in the "purple" family, mentioned in detail in Table 1 are lavender, violet-purple, violet, purple, purplish violet, reddish violet, and maroon.

Berry color is not only of great taxonomic significance in terms of species recognition, but it is also important in defining relationships between different groups of species. Fruit colors by percentage are summarized in Table 3. In Central America and the West Indies, red, orange, or yellow fruits predominate, while in South America, purple to purplish fruits predominate (Tables 2, 3). For example, for species with known fruit color in Mexico and Central America (excluding Costa Rica), 84% have red, orange, or yellow fruits (fruit color is not yet known for *A. sarukhanianum*, but its apparent relatives have fruits in this color range). In Costa Rica and Panama, this percentage is even higher (88%). Of these colors, orange predominates in Panama and Costa Rica, with 60% of the total. The orange-fruited species are in many ways atypical, often having leaves with long petioles and cordate to truncate or rounded bases. The red-fruited species, on the other hand, are more typical, with tight rosulate habits, short petioles, and generally acute leaf bases. Fruit color is still unknown in two Costa Rican or Panamanian species, i.e., *A. spathiphyllum* and *A. oerstedianum*. While the former is probably white-fruited, it is difficult to predict the fruit color of *A. oerstedianum* as it is seemingly unrelated to anything else. Central America has only one species with purple fruits, *A. fendleri*, which is a northern South American species barely reaching Central America (rare, in Panama only).

In contrast to Central America, South America, especially the lowland Amazonian basin, is rich in purple-fruited species (or fruits with at least some purple present), with 94% of the total in this category. The eastern slopes of the Andes are almost as rich in purplish fruited species, with 90% of the total being purple or with some form of purple. The western slopes of the Andes have a significantly lower percentage of purplish fruits (60%). This is largely due to the presence in the central Andes of series *Multinervia*, which has a large percentage of its species having orange fruits. The western slope of the Andes is more diverse in fruit color than the eastern slope, with fruits in the orange, red, and purple color groups. In contrast, the eastern or Amazonian slope has only the red and purple-fruited color groups. Of these color groups, purple still remains the most predominant, with the red to orange group having only 10%.

With the exception of the western Andean slopes and the far northern region of South America, purple fruits predominate in all other South American geographical areas. A total of 75% of the species of the Amazon Highlands and eastern Brazil are purplish fruited, while the comparable figures for the Guiana Highlands and the Andean Highlands are 100%. On the other hand, for species restricted to far northern South America (defined here as species with a range that includes lowlands with a Caribbean drainage), only 33% are purplish fruited. Indeed, of all species occurring in far northern South America (including those red-fruited species entering from Central America, *A. concolor* and *A. salviniae*) and in the West Indies (*A. cubense*), only 27% are purplish fruited. The only orange-fruited species not occurring in the central Andes or Costa Rica–Panama, *A. johnsoniae*, occurs in this region.

If all species with known fruit color occurring anywhere in South America are considered (including *A. affine*, which is also reported as sometimes red-fruited), a total of 46 out of 62 (74%) have purplish colored fruits, 12% have red fruits, and only 8% have orange fruits. Comparable figures for all species with known fruit color for Central America are 3% purple fruits, 29% red fruits, and 48% orange fruits. While the separation between purple-fruited species and those with red or orange fruits seems very clear, it is less obvious that there is a strong separation between red- and orange-fruited species. Though red and orange would intrinsically appear to be closely related colors, fruits of species in these color groups are typically conspicuously orange or conspicuously red. However, there are exceptions with *A. cubense* and *A. carchiense*, both of which have berries orange-red, and *A. purpureospathum*, with berries reported orange to red-orange or red. Both *A. cubense* and *A. purpurpeospathum* otherwise appear to be close relatives of red-fruited species of series *Pachyneurium*, while *A. carchiense* is otherwise closely related to other orange-fruited mem-

TABLE 1. Fruits, sorted by color

LOC	Species	Primary color*	Second color
CRP	*consobrinum*	white	greenish white
SBR	*coriaceum*	grayish white	lavender
MCA	*nizandense*	greenish white	
CRP	*acutifolium*	greenish yellow	
CRP	*bradeanum*	greenish yellow	white
CRP	*fatoense*	greenish yellow	orange, pale
MCA	*halmoorei*	yellow	
WA	*acutissimum*	yellow-orange	orange
WA	*angustilaminatum*	orange?	
CRP	*brenesii*	orange	
CRP	*colonicum*	orange	
CRP	*cotobrusii*	orange	
WA	*holmnielsenii*	orange	
NSA	*johnsoniae*	orange	
CRP	*luteynii*	orange	
CRP	*nervatum*	orange	
WA	*oxyphyllum*	orange	
CRP	*prolatum*	orange?	
CRP	*protensum*	orange	
CRP	*pseudospectabile*	orange	
CRP	*purpureospathum*	orange	red-orange
CRP	*ranchoanum*	orange	
CRP	*seibertii*	orange	
CRP	*spectabile*	orange?	
CRP	*standleyi*	orange	
CRP	*validifolium*	orange	
WA	*carchiense*	orange-red	
WCS	*cubense*	orange-red	
MCA	*salvadorense*	orange-red	
CRP	*schottianum*	pinkish?	
CAR	*venosum*	red-orange	
PSA	*concolor*	red	
NSA	*crassinervium*	red	
CRP	*eximium*	red	
EA	*fasciale*	red	
LA	*plowmanii*	red	
CSA	*salviniae*	red	
MCA	*schlechtendalii*	red	
WA	*sparreorum*	red	
CRP	*upalaense*	red	
NSA	*anorianum*	red, dark	
CAR	*crenatum*	red, bright	
BH	*affine*	red	purple maroon
WA	*lennartii*	red	purple, dark
CSA	*wagenerianum*	red	purple
EA	*latissimum*	maroon	red-violet, deep
EA	*paraguayense* var. *paraguayense*	maroon	reddish
GH	*wurdackii*	maroon	
LA	*ernestii* var. *ernestii*	red-violet	violet
LA	*uleanum* var. *uleanum*	reddish violet	
AH	*glaucospadix*	reddish purple	
WSA	*jenmanii*	reddish purple, pale	
EA	*reflexinervium*	reddish violet	
WA	*napeaum*	burgundy	purplish violet
LA	*willifordii*	magenta	
LA	*superbum*	lavender	

TABLE 1. Continued.

LOC	Species	Primary color*	Second color
LA	*pendulifolium*	lavender to white	
LA	*bonplandii* subsp. *bonplandii*	purple	
EA	*llewelynii*	purple	
WA	*obscurinervium*	purple	
LA	*oxycarpum*	purple	red
WA	*pallatangense*	purple	
EA	*paraguayense* var. *coroicoanum*	purple	
WA	*simpsonii*	purple	
BH	*solitarium*	purple	
LA	*loretense*	purple violet	
LA	*atropurpureum* var. *atropurpureum*	purple, dark	red, deep
AH	*leonianum*	purple, dark	
BH	*lindmanianum*	purple, dark	red, dark
WA	*palenquense*	purple, dark	
EA	*tarapotense*	purple, dark	
WA	*campii*	purple, light	
EA	*solomonii*	purple, pinkish	
GH	*bonplandii* subsp. *guayanum*	purple, reddish	purplish violet
LA	*remotigeniculatum*	purple, reddish	
WA	*barclayanum*	purplish	reddish brown
LA	*bonplandii* subsp. *cuatrecasii*	purplish?	
EA	*pachylaminum*	purplish?	
LA	*pranceanum*	violet	
LA	*uleanum* var. *nanayense*	violet	
LA	*vaupesianum*	violet	
LA	*atropurpureum* var. *arenicola*	violet-purple	
AH	*caucavallense*	violet-purple	
AH	*dombeyanum*	violet-purple	
LA	*ernestii* var. *oellgaardii*	violet-purple	
PSA	*fendleri*	violet-purple	reddish violet
EA	*harlingianum*	violet-red	purple, white
WA	*basirotundum*	wine red, deep	

* Primary = most frequently reported color.

Key to location codes: AH = Andean Highlands; BH = Brazilian Highlands; CAR = Caribbean; CRP = Costa Rica & Panama; CSA = Central & South America; EA = Eastern Andes; GH = Guiana Highlands; LA = Lowland Amazonas; MCA = Mexico & Central America; NSA = Northern South America; PSA = Panama & South America; SBR = S. Brazil; WA = Western Andes; WCS = West Indies, Central America, South America; WSA = West Indies & South America.

bers of series *Multinervia*. Thus, based on fruit color, there appears to be a clear separation between Central American and South American species of sect. *Pachyneurium*. This will be further discussed under breeding behavior (see Cytology section). White or yellow fruits are rare in sect. *Pachyneurium*. Yellow berries are known only for *A. halmoorei*, an isolated species from western Mexico. Whitish berries are known only for *A. nizandense* from Mexico, *A. bradeanum* from Costa Rica and Panama, and *A. coriaceum* from southern Brazil. None of the above species are closely related.

Seeds. Like those of most species of *Anthurium*, the seeds of sect. *Pachyneurium* are one per locule, though one frequently aborts, leaving a one-seeded fruit. Seeds are commonly oblong or oblong-elliptic and are weakly flattened with the basal end rounded and the apical end obtusely notched where the funicle is attached. Typically, seeds are attached to the inner surface of the carpel wall by means of a slender mucilaginous strand, and one or both ends may bear a sticky, usually amber-colored appendage, which aids in dispersal. Sometimes the entire seed is enveloped in a mucilaginous envelope, which may protrude at both ends. A more uncom-

TABLE 2. Fruit colors in *Pachyneurium* by locality.

	Pachyneurium fruit colors				
	Yellowish, greenish yellow	Greenish, greenish white, white, cream	Orange, red-orange	Red, reddish, orange-red	Purple, red-purple, maroon, violet
Mexico & Central America (excluding Costa Rica & Panama)	*halmoorei*	*nizandense*		*cubense**	
				salvadorense	
				schlechtendalii	
				subsp. *schlechtendalii*	
				subsp. *jiminezii*	
Costa Rica & Panama	*acutifolium*	*consobrinum*	*brenesii*	*concolor*	
	bradeanum		*colonicum*		
	fatoense		*cotobrusii*	*cubense**	
			luteynii	*eximium*	
			nervatum		
			prolatum	*schottianum*	
			protensum	*upalaense*	*fendleri**
			subsp. *protensum*		
			subsp. *arcuatum*		
			pseudospectabile		
			purpureospathum		
			ranchoanum		
			seibertii		
			spectabile		
			standleyi		
			validifolium		
Central America/northern South America				*salviniae*	
Northern South America	*johnsoniae*		*anorianum*	*fendleri*	
			*concolor**	*jenmanii*	
			crassinervium		
West Indies & Circum-Caribbean	*venosum*		*crenatum*	*jenmanii**	
Caribbean South America			*cubense*		
	*cubense**				*wagenerianum*

TABLE 2. Continued.

	Pachyneurium fruit colors				
	Yellowish, greenish yellow	Greenish, greenish white, white, cream	Orange, red-orange	Red, reddish, orange-red	Purple, red-purple, maroon, violet
Lowland Amazon Basin				*plowmannii*	*atropurpureum* var. *atropurpureum* var. *arenicola* *bonplandii* subsp. *bonplandii* subsp. *cuatrecasii* *ernestii* var. *ernestii* var. *oellgaardii* *loretense* *oxycarpum* *uleanum* var. *uleanum* var. *nanayense* *willifordii* *pendulifolium* *pranceanum* *remotigeniculum* *superbum* *vaupesianum*
Eastern slopes of Andes Mountains			*fasciale*		*harlingianum* *latissimum* *llewelynii* *pachylaminum* *paraguayense* var. *coroicoanum* var. *paraguayense* *reflexinervium* *solomonii* *tarapotense*

TABLE 2. Continued.

	Pachyneurium fruit colors				
	Yellowish, greenish yellow	Greenish, greenish white, white, cream	Orange, red-orange	Red, reddish, orange-red	Purple, red-purple, maroon, violet
Western slopes of Andes Mountains			*acutissimum* *angustilaminatum* *holmnielsenii* *oxyphyllum*	*carchiense* *sparreorum*	*barclayanum* *basirotundum* *campii* *lennartii* *napeaum* *obscurinervium* *pallenquense* *pallatanguense* *simpsonii*
Brazilian Highlands					*affine* *lindmanianum*
Lowland southern Brazil		*coriaceum*			*solitarium*
Guiana Highlands					*bonplandii* subsp. *guayanum* *wurdackii*

* Species primarily from another geographical region, but present here as well.

TABLE 3. Fruit color percentages by region.

	Fruit colors % by location					
	Yellowish, greenish yellow	Greenish, greenish white, white, cream	Orange, red-orange	Red, reddish, orange-red	Purple, red-purple, maroon, violet	Total number of species
Mexico & Central America						
excluding Costa Rica & Panama	17%	17%		67%		6
Costa Rica & Panama	8%	8%	60%	20%	4%	25
Central & northern South America				100%		1
Northern South America			17%	50%	33%	6
West Indies & Caribbean			25%	50%	25%	4
Caribbean South America			50%		50%	2
Lowland Amazonas				6%	94%	17
Eastern Andes				10%	90%	10
Western Andes			27%	13%	60%	15
Brazilian Highlands				25%	75%	4
Lowland southern Brazil		100%				1
Andean Highlands				25%	75%	4
Guiana Highlands					100%	2
Total number of species	3	4	22	21	47	97

mon type of seed attachment is found in *A. bonplandii* and *A. wagenerianum*, where the seeds are attached by their apical end to the inner carpel wall by a thick strand of fibers running down the carpel wall toward the base of the fruit.

FRUITING BEHAVIOR

The production of fruits in *Anthurium* is generally similar for all sections, with the pistil and the tepals gradually enlarging in unison after pollination. Some species, e.g., *A. consobrinum* and *A. colonicum*, have fruits that develop from an early-emergent pistil. In these cases, the pistil remains green until shortly before fruit maturation. In most species the developing fruit remains below the level of the tepals until very near the time of fruit maturation, or they emerge somewhat above the level of the tepals but remain uncolored. Shortly after anthesis the tepals generally begin to lose their coloration, often turning brownish, or they may become green and presumably photosynthetic. Coloration of fruits usually begins in the last one-third of their development, but may proceed slowly or promptly. Generally the berries remain firm even after full coloration, and for weeks before they begin to soften and loosen. In most species the softening of individual fruits is only partial and is widely scattered on the infructescence. The softened and generally plumper berries begin to emerge and may even be extruded and supported by threadlike tepalar fibers (narrow strips of epidermis from the inner surface of the tepals). This form of display broadens the visual target of the infructescence for bird dispersers and makes picking off the fruits much easier. In other cases, the mature berries are not extruded but merely become loosened and, if not removed, simply fall to the ground. Many examples have been seen where animals have fed on the infructescence only to leave the seeds scattered beneath the plant. Because the seeds are sticky, many even stick to the leaves of the same plant or other plants in the immediate vicinity.

By the time fruits are mature the tepals may have expanded to more than twice their original length, and the outer surface of the tepal (the only part regularly visible) may be expanded to a lesser extent, but they remain in appearance very much like they were originally. An exception to this occurs in *A. sparreorum*, which develops fruits in an almost unique manner for *Anthurium* (seen elsewhere only in an unidentified Ecuadorian member of sect. *Belolonchium*). In this species, the apical part of the tepal greatly expands and becomes white and fleshy, in reality taking on a role in fruit dispersal ecology since the fruits, though red at maturity, barely emerge above the tepals. Despite the fact that the fruits are not prominently exserted in the manner of other sect. *Pachyneurium* species, the red mature fruits are highly visible since they are displayed between the fleshy white tepals.

In most *Pachyneurium* species the infructescence is straight at maturity, but some taxa, such as *A. atropurpureum* and *A. pendulifolium*, may

have a coiled infructescence when fully developed. This may serve to provide a more compact visual display to better attract dispersers, or perhaps it serves to spread out the time over which mature fruits are available for distribution by providing fewer fruits that are readily accessible at any time.

The amount of time required for fruits to develop varies greatly from species to species and may apparently vary considerably within each species as well (at least under greenhouse conditions). For species of sect. *Pachyneurium*, fruit development time under greenhouse conditions vary from as little as 3 months (for *A. llewelynii*) to as much as 13 months (for *A. salvadorense*). Fruit development time may vary greatly on successive pollinations. For example, fruit development time on *A. schlechtendalii* (see below) varied from 4.5 to 11 months, and on *A. upalaense* from 6 to 13 months, while *A. halmoorei* varied from 8.5 to 12 months.

Fruit development time

Species	Months to maturity (number of inflorescences observed)
A. atropurpureum arenicola	4 (2); 4.5 (4); 5 (1); 5.5 (2)
A. atropurpureum atropurpureum	9.5 (1)
A. barclayanum	12.5 (1); 13 (1)
A. colonicum	11 (2)
A. consobrinum	6 (1)
A. crassinervium	4.5 (1); 10.5 (1)
A. cubense	4.5 (1); 5 (1)
A. fendleri	10.5 (1); 11 (1); 11.5 (1)
A. halmoorei	8.5 (1); 9 (1); 10 (1); 11.5 (1); 12 (1)
A. llewelynii	3 (1)
A. luteynii	10 (1); 10.5 (1); 11 (1)
A. paraguayense	4 (1)
A. salvadorense	13 (1); 13.5; 15 (1)
A. schlechtendalii	4.5 (1); 11 (1)
A. standleyi	11 (1)
A. upalaense	6 (1); 7 (1); 13 (1)

PHENOLOGY

A phenological survey of greenhouse collections was undertaken by volunteer researcher Edwina Medlock. The study was carried out over a two-year period beginning November 1979 and ending in October 1981. Plants were observed on a weekly basis, and the initiation of new leaves and inflorescences was recorded. A total of 38 taxa of *Pachyneurium* was studied. The taxa involved in the study and the number of individuals of each species were as follows:

Anthurium affine	4	*A. nervatum*	1
A. angustilaminatum subsp. *angustilaminatum*	2	*A. oerstedianum*	2
A. barclayanum	1	*A. oxycarpum*	1
A. bradeanum	1	*A. plowmanii*	1
A. brenesii	2	*A. protensum* subsp. *arcuatum*	2
A. colonicum	2	subsp. *protensum*	2
A. concolor	1	*A. pseudospectabile*	1
A. consobrinum	2	*A. purpureospathum*	2
A. coriaceum	1	*A. salvadorense*	3
A. cotobrusii	2	*A. salviniae*	3
A. crassinervium	2	*A. schlechtendalii* subsp. *jimenezii*	1
A. crenatum	2	subsp. *schlechtendalii*	2
A. cubense	2	*A. schottianum*	2
A. eximium	1	*A. seibertii*	2
A. fatoense	2	*A. spathiphyllum*	2
A. fendleri	2	*A. standleyi*	2
A. halmoorei	2	*A. upalaense*	2
A. jenmanii	3	*A. validifolium*	1
A. luteynii	2	*A. watermaliense*	1

The following is a summary of the results of the survey.

Leaf production. Though many factors are involved in the production of both vegetative and fertile plant parts, including growing conditions (especially the amount of available light, nutrients, and humidity, as well as the general health of the plant), the collections were in general growing under moderately uniform conditions and were housed in the same room. Obviously some plants, owing to their larger size, received more light. The study showed that substantially more leaf production occurred during long daylength time periods (March to September) than during short daylength time periods. Though the greenhouse was heated, the nighttime temperature was allowed to drop to 65°F during the winter months, whereas in the warmer summer months the nighttime temperature often did not drop so low. Equally important, the daytime temperatures in the summer months were often very high, occasionally reaching 80°F, whereas in the cooler months such temperatures would have been rare.

During long days (March–September), a group of 71 individual study plants of sect. *Pachyneurium* produced an average of 120 leaves for the group per year, whereas during short days (September–February) the study plants produced only 94 leaves. Each of the study plants produced on the average four leaves per year during the two year study, but the range of new leaves produced

was one new leaf per year produced on *A. pendulifolium* to 10 new leaves per year for *A. standleyi*. Plants performed better the first year of the study, producing an average of 4.5 leaves per year vs. 3.4 leaves per year during the second year. This was no doubt due to the increasing size of the plants and the fact that the larger the plants got the more they shaded one another, causing the poorer growers to obtain increasingly less light. The interval between leaf production was highly variable, with the minimum time between the production of new leaves ranging from 1 to 16 weeks (averaging 3 weeks), and the maximum interval between the production of new leaves ranging from 8 to 46 weeks (averaging 25.4). Production of new leaves was highly variable throughout the year for most species, with major leaf production activity between March and September. The maximum number of leaves produced during the two-year study was during March (a total of 56 over 2 years), and the minimum were produced during February and October (a total of 18 for each month). Frequently, most of the leaves produced by an individual were produced during the 4- or 5-month period following the initial burst in March. Another period that was important for some species was January, with one or more leaves being produced at that time (Fig. 22). The initiation of leaf production during the early months of the year is probably best explained by the fact that these months have increasingly longer days following a period of decreasing daylight in the late fall. Plants generally go through a period of low leaf production in the late fall when days are getting shorter, especially between September and December. The burst of activity in January is unusual since leaf production dropped off again in February only to increase once more in March (Fig. 22). During the period of maximum leaf production it is not uncommon for leaves on a single plant to be produced at the rate of one per week, though a period of two to three weeks between leaves is more common. Leaf production is greatest on younger plants and tends to slow after the plant has reached a more mature size. Leaf production can be markedly sporadic. For example, one plant of *A. brenesii* produced seven leaves in a 5-month period one year (March to July), then after producing one leaf in November, it did not produce another leaf until the following September. Leaf production on some species can be very slow. For example, an individual of *A. pendulifolium* (not included in the study) failed to produce a single leaf in more than a year, despite the fact that the plant appeared to be in good health and even flowered during this period. In general, healthy, robust plants produced more leaves than smaller or unhealthy plants, and there was a high correlation between leaf production and the amount of fertilizer applied, with most plants responding to increased fertilizer by growing faster and producing more leaves.

Flower production. Because each leaf axil ultimately produces an inflorescence on adult plants of *Anthurium*, the production of inflorescences on *Pachyneurium* closely follows the activity described for leaf production (Fig. 22), with the peak flowering activity also being in March, followed by a marked diminution until about June. During the warmer months flowering reaches an almost steady state, with 13–17 inflorescences produced each month between June and November for the 2-year period. As with leaf production, December and January show a spurt of flowering activity, with a trough in February, followed by a major spurt of activity in March. As with leaf production, the interval between inflorescence production is highly variable but does not necessarily follow the same pattern. Some species produce their inflorescences from the axil of the newly formed leaves shortly after the leaf emerges, whereas other species delay the production of new inflorescences for several weeks or even months after the new leaf emerges. The minimum average interval between the production of new inflorescences for all species in the 2-year study was 1.7 weeks (ranging from 1 to 14 weeks). The average maximum interval between the production of successive inflorescences was 29 weeks (ranging from 7 to 46 weeks). The duration of flowering for any single inflorescence is also highly variable, with some species flowering for a period of less than one week and others (such as *A. luteynii* and *A. salviniae*) flowering for a month or more. For a discussion of the phenology of fruit production, see the section on Fruiting Behavior.

CYTOLOGY By R. D. Sheffer

Species of sect. *Pachyneurium* are predominantly diploids with chromosome counts of $2n = 30$ and with fewer numbers of species being tetraploids with $2n = 60$ chromosomes. This corresponds to the most common number in the genus as a whole (Sheffer & Croat, 1983). While not all species have been counted, R. D. Sheffer has made chromosome counts on many of the species not previously covered in earlier publications. He reports (pers. comm.) that a few species do not fit the usual pattern. *Anthurium ranchoanum*, with two collections counted (*Croat 49846* and *Stevens*

13980), has a chromosome count of $2n = 44$. *Anthurium atropurpureum* var. *arenicola* exhibits aneuploidy at the tetraploid level.

An analysis done by Sheffer on a country by country basis indicates that there is a statistically significant difference between the number of polyploids in Central and South America. South America has more polyploids (41.3%) than Central America (10.7%). This suggests that the South American species are older and thus South America probably represents the center of origin of the section. This is borne out by the fact that the South American continent (especially the western edge of the Amazon basin and the foothills of the Andes in Ecuador and Peru) is also the area of greatest speciation in the group (see section on Geographical Distribution).

BREEDING BEHAVIOR (with R. D. Sheffer)

Breeding studies carried out by Sheffer at the Indiana University Northwest and by Croat at the Missouri Botanical Garden indicate that sect. *Pachyneurium* is probably reproductively isolated. Crossability between sect. *Pachyneurium* and other sections of the genus is very limited. Thus far there are only two examples of successful outcrossing with another section of *Anthurium* that resulted in the production of viable seedlings. These crosses were between the *Pachyneurium* species *A. standleyi* and *A. lilacinum*, a member of sect. *Urospadix* as well as *A. hacumense* (sect. *Porphyrochitonium*) and *A. glaucospadix* (sect. *Pachyneurium*). Though these were the only examples of crossability which produced viable seeds, studies show that there is potential crossability with other sections, if only fruit-set or seed production is considered as a significant measure of species relationship. Of the 433 cross-pollinations, 33 (7.4%) resulted in fruit-set and 28 (6.3%) resulted in seed production. These crosses were between sect. *Pachyneurium* and five other sections, *Belolonchium*, *Cardiolonchium*, *Dactylophyllium*, *Porphyrochitonium* and *Urospadix*. All, except the cases mentioned above (sects. *Urospadix* and *Porphyrochitonium*), resulted in abortive seeds that failed to germinate. This is further evidence that sect. *Pachyneurium* is reproductively isolated from other sections.

Besides being reproductively isolated from other sections of the genus, Central and South American species of sect. *Pachyneurium* are mostly reproductively isolated from one another. A total of 747 cross-pollinations within the section resulted in 116 (15.5%) with fruit-set and 88 (12%) with viable seedlings, which are probably hybrids (e.g., not merely cases of self-inducement to set fruits). Most of the pollinations that resulted in viable seedlings were among either Central American species or among South American species, but not between the respective groups. Thus, the Central American and South American species appear virtually isolated reproductively. Exceptions to the failure of crossability between Central and South American taxa are between *A. barclayanum* (Ecuador) and *A. cotobrusii* (Costa Rica and Panama), *A. crassinervium* (Venezuela) and *A. bradeanum* (Nicaragua–Panama). Also worthy of mention are two viable crosses between *A. halmoorei* (Mexico) and *A. fendleri*, which is largely from northern South America but also ranges into central Panama.

However, if production of fruits without viable seed is also considered, then two additional Central American vs. South American crosses become important. These were crosses between *A. halmoorei* and *A. uleanum* and between *A. halmoorei* and *A. latissimum*.

Other crosses that might prove viable (producing infructescences but as yet without mature fruits) are two South American species, *A. atropurpureum* var. *arenicola* and *A. harlingianum*, both of which seem to have crossed successfully with *A. nervatum* from Panama. Similarly, *A. bonplandii* subsp. *cuatrecasii* (South America) seems to have successfully crossed with both *A. halmoorei* (Mexico) and *A. purpureospathum* (Panama).

Anthurium crenatum, a West Indian species, shows apparent relationship with Central and South America, having been used in partially successful crosses (fruit matured but seeds inviable) with *A. halmoorei* (Mexico) and *A. fendleri* (northern South America and Panama), and also *A. glaucospadix* and *A. paraguayense* of South America.

Sheffer's study also indicates there may be limited interspecific gene flow throughout Central and South America, since 36% (27) of the 74 species tested by him have been involved in interspecific crosses that resulted in viable seed (seedlings viable or not).

While we have not attempted all possible crosses between different species of sect. *Pachyneurium*, the lists below summarize the successful crosses of the 226 cross-pollination attempts (including repeats of the same cross). The crosses involve 58 different taxa, of which 27 were successfully involved in crosses (produced viable plants).

Successful crosses of Central American species of *Pachyneurium*

A. consobrinum × *A. upalaense*
A. luteynii × *A. colonicum*

A. luteynii × *A. purpureospathum*
A. schlechtendalii × *A. salviniae*
A. schlechtendalii × *A. luteynii*
A. schlechtendalii × *A. upalaense*
A. standleyi × *A. halmoorei*
A. upalaense × *A. halmoorei*
A. upalaense × *A. purpureospathum*

Successful crosses of South American species of *Pachyneurium*

A. atropurpureum arenicola × *A. ernestii*
A. atropurpureum atropurpureum × *A. atropurpureum arenicola*
A. barclayanum × *A. atropurpureum arenicola*
A. barclayanum × *A. glaucospadix*
A. crassinervium × *A. barclayanum*
A. cubense × *A. atropurpureum arenicola*
A. fendleri × *A. atropurpureum arenicola*
A. fendleri × *A. remotigeniculatum*
A. harlingianum × *A. oxycarpum*
A. llewelynii × *A. ernestii*
A. paraguayense × *A. llewelynii*
A. tarapotense × *A. plowmanii*

GEOGRAPHICAL DISTRIBUTION

The geographical distribution of *Anthurium* sect. *Pachyneurium* is summarized in the geographical checklist in Appendix 4. Although sect. *Pachyneurium* is widely dispersed throughout the Neotropics, ranging from Mexico to the West Indies and south to Argentina (from ca. 22° north to ca. 27° south), there are major centers of speciation. Species diversity is greatest from Costa Rica to Peru, with a major center in Ecuador (36 spp.) and to a lesser extent in Peru (28 spp.), and with minor centers in Costa Rica and Panama (both with 23 spp.), and the Guiana region (14 spp.), mostly in Venezuela.

A detailed analysis of the geographical distribution of *Anthurium* sect. *Pachyneurium* by area follows:

Mexico. This area is important as an area of local endemism (see section on Centers of Endemism below), with five of its seven taxa endemic. One wide-ranging species, *A. schlechtendalii*, consists of two subspecies ranging down either coast with an extension of the typical subspecies into Nicaragua. Another species, *A. salviniae*, extends from the moist forests on the Pacific slope of Chiapas to Colombia, while the remaining five species are endemic. One, *A. halmoorei*, is restricted to Michoacán, Nayarit, and Jalisco on the Pacific coast, while *A. nizandense* is found in Oaxaca and Guerrero. Along with *A. sarukhanianum*, endemic to Michoacán, these species occur in dry habitats as does *A. schlechtendalii* subsp. *jimenezii*, which is widespread on the Pacific coast. The fifth endemic species, *A. machetioides*, occurs in the humid Chinantla region of northeastern Oaxaca.

Central America (excluding Costa Rica and the wet southeastern corner of Nicaragua). This region is remarkably low in species, with only *A. cubense* (a species better known from the West Indies and northern Venezuela and inhabiting only the drier areas), *A. salvadorense* (from dry areas in northern El Salvador and adjacent Guatemala), *A. salviniae*, and *A. schlechtendalii* (present throughout most of this range). The latter two are the only widespread species. Four additional species occur in Nicaragua, *A. consobrinum*, *A. bradeanum*, *A. spathiphyllum*, and *A. upalaense*, but only the last extends much beyond the wet southeastern corner of the country.

Costa Rica. This country is a minor center of endemism and is rich in species diversity. While most species occur in the wet Atlantic lowlands or at higher elevations in the Cordillera de Talamanca (including *A. brenesii*, *A. bradeanum*, *A. consobrinum*, *A. fatoense*, *A. protensum*, *A. ranchoanum*, *A. schottianum*, *A. spectabile*, and *A. upalaense*), several taxa are restricted to the Pacific coast. *Anthurium cubense* occupies only dry areas of Guanacaste and Puntarenas provinces. Several species are restricted to the Pacific slope in the southeastern part of the country, mostly in the vicinity of the Osa Peninsula. These include *A. acutifolium* var. *acutifolium*, *A. acutifolium* var. *herrerae*, *A. eximium*, *A. oerstedianum*, and *A. standleyi*. Only *A. salviniae* is relatively widespread on both the Atlantic and Pacific watersheds.

In addition to being high in species diversity of sect. *Pachyneurium*, Costa Rica is also rich in endemism, with 7 of 23 species endemic. The endemics are *A. acutifolium* var. *herrerae*, *A. brenesii*, *A. eximium*, *A. oerstedianum*, *A. schottianum*, *A. spectabile*, and *A. standleyi*.

Panama. While Panama is similar to Costa Rica in having most of its species of *Pachyneurium* restricted to the Atlantic slopes, more species straddle the Continental Divide than in Costa Rica. Few species are restricted to lower elevations along the Atlantic coast (*A. concolor* and *A. spathiphyllum*), but among those primarily restricted to the Atlantic slope and to the ridges near the Continental Divide on the Pacific slope are *A. bradeanum*, *A. coloni-cum*, *A. consobrinum*, *A. hammelii*, *A. pseudospectabile*, *A. purpureospathum*, *A. ranchoanum*, *A. seibertii*, and *A. validifolium*. Three species

are restricted to the Pacific slope, *A. acutifolium* (Burica Peninsula), *A. cubense* (lowland Chiriquí), and *A. fendleri* (Coclé). As in Costa Rica, *A. salviniae* is distributed widely on both the Atlantic and Pacific slopes. Four species are found on both slopes near the Continental Divide. These are *A. luteynii*, *A. nervatum*, *A. protensum* subsp. *arcuatum*, and *A. pseudospectabile*.

Panama is one of the major centers of endemism in Central America, being about as rich in endemics as Costa Rica, with 5 of 22 species endemic. Endemic species are *A. colonicum*, *A. hammelii*, *A. luteynii*, *A. nervatum*, *A. pseudospectabile*, and *A. purpureospathum*.

Colombia. The *Pachyneurium* species of Colombia are widely dispersed with no particular areas of species diversity. A few species are widespread and range into the country from Central America, the West Indies, or Venezuela. These include *A. salviniae*, which ranges from southern Mexico to the upper Magdalena River Valley in south-central Colombia; *A. fendleri* and *A. crassinervium*, which enter from northern and western Venezuela; and *A. cubense*, which ranges throughout the western periphery of the Caribbean. An additional species, *A. concolor*, enters the north from Panama. There are two endemic species inhabiting the northern part of the country, *A. johnsoniae*, from the Sierra de Santa Marta, and *A. anorianum* from northern Antioquia. Two additional and more widespread endemics occur in the central highlands of the country, *A. caucavallense* and *A. glaucospadix*.

The majority of *Pachyneurium* taxa from Colombia occur in the Amazon basin in the southern part of the country. These include *A. atropurpureum* var. *atropurpureum*, *A. atropurpureum* var. *arenicola*, *A. bonplandii* subsp. *bonplandii*, *A. bonplandii* subsp. *cuatrescasii*, *A. galactospadix*, *A. harlingianum*, *A. loretense*, *A. oxycarpum*, *A. pendulifolium*, and *A. vaupesianum*. Of these only *A. vaupesianum* is restricted to Colombia, the remainder being relatively widespread in the Amazon basin.

It is interesting that while Colombia has the greatest species diversity for the genus as a whole, possibly with as many species of *Anthurium* as all the rest of Latin America put together, it is not particularly rich in sect. *Pachyneurium*. This owes to the fact that most of the species diversity for the genus is in the wettest part of the country along the Pacific coast, while the more mesic parts of the country have been long deforested and are isolated from the apparent center of species diversity for sect. *Pachyneurium*, namely Amazonian Ecuador and Peru. Only four species of *Pachyneurium* occur on the otherwise aroid-rich Pacific slope of Colombia. One of these, *A. caucavallense*, laps over the Divide of the Eastern Cordillera in Valle, occurring only on dry upland slopes, and is a member of series *Pachyneurium*. Three other species, *A. carchiense*, *A. napaeum*, and *A. narinoense*, all members of series *Multinervia*, occur in wetter areas in Nariño. Though it is not unusual that there are no representatives of series *Pachyneurium* from the wet Pacific slope (since they prefer drier habitats), it is unusual that so few members of series *Multinervia* (a group preferring mesic habitats) occur there. It is particularly curious that only three of the species in series *Multinervia* occur in this part of Colombia, since there would appear to be numerous suitable habitats for these mesic taxa in southwestern Colombia in Nariño, Cauca, and Valle. Perhaps further collecting in these poorly known areas of Colombia will turn up additional species or records for this group. The area is still largely unexplored. Colombia has relatively few endemic species, with only 6 of 24 endemic. These are *A. anorianum*, *A. caucavallense*, *A. glaucospadix*, *A. johnsoniae*, *A. narinoense*, and *A. vaupesianum*.

Ecuador. Along with Peru, this area represents the major center of diversity for taxa of sect. *Pachyneurium*, with species concentrated primarily in the Amazon lowlands of both countries and on both slopes of the Andes in Ecuador. Considering its relatively small size compared to the surrounding countries, Ecuador is clearly the richest country in species diversity. The country is broken up into several different phytogeographical regions, but each contributes a considerable share of the total number of species. Those taxa that occur principally in the Amazonian lowlands are *A. atropurpureum* var. *arenicola*, *A. ernestii*, *A. pendulifolium*, *A. superbum*, *A. tenaense*, and *A. uleanum*. Several other species occur only on the eastern slopes of the Andes but at higher elevations, usually above 500 m. These include *A. bushii*, *A. harlingianum*, *A. penningtonii*, and *A. santiagoense*. *Anthurium bushii* and *A. santiagoense* are restricted to the Río Santiago drainage system. *Anthurium oxycarpum* is wide-ranging, extending from the lowlands up to 850 m.

Only two species, *A. dombeyanum* and *A. leonianum*, occur in the drier highland regions of Ecuador. Most of the remaining species of sect. *Pachyneurium* in Ecuador are restricted to the Pacific slope. In this respect Ecuador is radically different from Colombia, since only three species

of *Pachyneurium* occur on the wet Pacific slope in Colombia. Species that occur at lower elevations on the Pacific slope include *A. asplundii*, *A. barclayanum*, *A. linguifolium*, *A. manabianum*, *A. napaeum*, and *A. sparreorum*. No species is known to occur on both slopes of the Andes. This is not unusual considering the age of the Andes and the broad stretch of cold, arid, and generally inhospitable land lying between the mesic slopes to the east and west.

Ecuador has the largest number (36), as well as the highest concentration of endemic *Pachyneurium* species of any country, the endemics constituting more than half of the total species. Many of the endemics are members of series *Multinervia* and include *A. acutissimum*, *A. angustilaminatum*, *A. fasciale*, *A. holmnielsenii*, *A. lennartii*, *A. napaeum*, *A. oxyphyllum*, *A. palenquense*, *A. pallatangense*, *A. penningtonii*, and *A. santiagoense*. Series *Multinervia* is almost endemic to Ecuador, with only three species, *A. carchiense*, *A. napaeum*, and *A. narinoense*, occurring in southwestern Colombia, and two species, *A. soukupii* and *A. ottonis*, occurring to the south in Peru and Bolivia.

Peru. Peru is the second richest country for species of sect. *Pachyneurium*. If only the members of series *Pachyneurium* are considered, Peru is actually richer than Ecuador because about one-third of the Ecuadorian members of the section are members of series *Multinervia*. Most species of series *Multinervia* occur in Ecuador, while relatively few occur in adjacent countries. Nearly all of the Peruvian species of sect. *Pachyneurium* are members of series *Pachyneurium*. The vast majority of Peruvian *Pachyneurium* species occur on the eastern slope of the Andes and in the Amazon lowlands. Taxa occurring in the lowlands of the Amazon basin include *A. atropurpureum* var. *atropurpureum*, *A. atropurpureum* var. *arenicola*, *A. galactospadix*, *A. loretense*, *A. manuanum*, *A. penduliifolium*, *A. superbum* subsp. *brentberlinii*, *A. uleanum* var. *nanayense*, and *A. willifordii*.

Almost an equal number of species occurs in the foothills of the Andes at medium elevations (300–1,000 m). These include *A. basirotundum*, *A. harlingianum*, *A. knappiae*, *A. latissimum*, *A. llewelynii*, *A. manuanum*, *A. pachylaminum*, *A. reflexinervium*, *A. remotigeniculatum*, and *A. tarapotense*. The majority of these species are from the northern half of Peru, especially in the departments of Amazonas, San Martín, and Huánuco. Areas of particularly high concentration of *Pachyneurium* are the areas around Tingo María in Huánuco Department, and around Tocache Nuevo and Tarapoto in San Martín Department. The Tarapoto vicinity, for example, has no fewer than five *Pachyneurium* species.

Several other species are restricted to the eastern slopes of the Andes and in the Amazon lowlands but are more wide-ranging in elevation, occurring in the lowlands and in the foothills of the Andes. These include *A. ernestii*, *A. oxycarpum*, and *A. plowmanii*.

Two species, *A. dombeyanum* and *A. soukupii*, are restricted to higher elevations in Peru and range from Cusco Department in the south to Amazonas Department in the north. While the former occupies mostly dry life zones, the latter inhabits generally wetter sites in various montane forest life zones. One species, *A. ottonis*, occurs at higher elevations in the far south of Peru in Puyo Department, as well as in adjacent Bolivia. Two species, *A. barclayanum* and *A. simpsonii*, are restricted to the moist forests of the Pacific slope of northwestern Peru in Tumbes Department.

After Ecuador, Peru has the greatest concentration of series *Pachyneurium* taxa. It also has the second highest concentration of endemic species, with 13 of 28 endemic taxa. These are: *A. basirotundum*, *A. knappiae*, *A. latissimum*, *A. llewelynii*, *A. manuanum*, *A. pachylaminum*, *A. reflexinervium*, *A. remotigeniculatum*, *A. simpsonii*, *A. superbum* subsp. *brentberlinii*, *A. tarapotense*, *A. uleanum* var. *nanayense*, and *A. willifordii*.

Bolivia, Paraguay, and Argentina. A total of nine taxa inhabit this southern, subtropical and temperate region of South America. The only species common to all three countries is *A. paraguayense* (also in southern Mato Grosso in Brazil), and only Bolivia has endemic taxa, *A. atropurpureum* var. *thomasii* and *A. solomonii*. *Anthurium paraguayense* ranges the furthest south of all members of sect. *Pachyneurium* and is the only member of the section in Argentina. One species, *A. plowmanii*, is common to both Paraguay and Bolivia, occurring in the Amazon lowlands with its southern extension in central Paraguay. Bolivia, the most tropical of the three countries, is the richest in species, with nine taxa. These are: *A. atropurpureum* var. *arenicola*, *A. atropurpureum* var. *thomasii*, *A. ottonis*, *A. oxycarpum*, *A. paraguayense* var. *paraguayense*, *A. paraguayense* var. *coroicoanum*, *A. plowmanii*, *A. solomonii*, and *A. soukupii*. In Bolivia (in contrast to its range in Peru), *A. oxycarpum* occurs only in the lowlands in El Beni Province. *Anthurium atropurpureum*

var. *arenicola* is also a lowland species, known from La Paz Department at less than 20 m. *Anthurium atropurpureum* var. *thomasii* occurs at about 750 m in the isolated Serranía de Huanchaca, near the eastern border of the country. *Anthurium plowmanii* ranges from the lowlands of Bolivia to 900 m in Santa Cruz Department. *Anthurium paraguayense*, entering Bolivia from more temperate Argentina and Paraguay, ranges very widely in Bolivia, occurring from 200 to 1,700 m. The remaining four Bolivian species, *A. ottonis*, *A. paraguayense* var. *coroicoanum*, *A. solomonii*, and *A. soukupii*, occur only at higher elevations, all being known only from the Yungas in the Department of La Paz at 800 to 2,200 m.

Brazil. Brazil, with 18 species, is relatively rich in species, but considering the broad area encompassed and that the species are not concentrated in any particular area, it is not important as a center of species diversity. The *Pachyneurium* species of Brazil are generally widely dispersed except in the upper Amazon region, especially in Acre, where as many as four species can be found in a small area. Elsewhere, in general, no more than one or two species are present at any site and may be scarce when present. The area of greatest concentration of species in Brazil is in the upper Amazon region in the western part of the states of Amazonas and Acre. This is understandable since, in general, species diversity for the family increases in the Amazon basin as one approaches the Andes from the Amazon lowlands and is probably greatest at 500 to 1,500 m on the Andean slopes. Taxa that are restricted to the western Amazon basin in Brazil include *A. atropurpureum* var. *atropurpureum*, *A. atropurpureum* var. *arenicola*, *A. ernestii* var. *ernestii*, *A. galactospadix*, *A. krukovii*, *A. oxycarpum*, *A. pranceanum*, and *A. uleanum*. Another species, *A. plowmanii*, occurs in the same region as well, but extends much further to the east, ranging throughout the Amazon basin to Manaus, as well as east to Mato Grosso and south to Rondônia and Acre. Two species are restricted to the upland regions of central Brazil south of Pernambuco and south of the Amazon basin. One of these, *A. affine*, ranges from Minas Gerais to Pernambuco, south to Mato Grosso do Sul and Espíritu Santo, but is centered mainly in Bahía. The other species, *A. lindmanianum*, ranges from Pará, south to Rondônia, Mato Grosso, and Goiás.

Two species, *A. coriaceum* and *A. solitarium*, occur in southeastern Brazil, in southern Minas Gerais, Espíritu Santo, Paraná, Guanabara, and Rio de Janiero states. They commonly occur on rocks in seasonally dry areas with scrubby vegetation. One species, *A. paraguayense*, occurs in southeastern Brazil in Mato Grosso do Sul near the Paraguay border. Three species occur in northern Brazil. One of these, *A. bonplandii* subsp. *bonplandii*, is wide-ranging, occurring principally north of the Amazon River, and extending from the border with Peru to north-central Pará State, but is also sparsely distributed to the south of the Amazon River in the states of Amazonas and Pará. The other two species, *A. jenmanii* and *A. cataniapoense*, occur only in northeastern Brazil in Amapá and Pará, respectively. Both range into Brazil from Venezuela or the Guianas.

One-third of the Brazilian species are endemic to Brazil. These include *A. affine*, *A. coriaceum*, *A. krukovii*, *A. lindmanianum*, *A. pranceanum*, and *A. solitarium*.

Venezuela. The Venezuelan species can be for the most part separated geographically and can occupy diverse phytogeographical regions including the northern Amazon basin, the Guiana Highlands, the northeastern periphery as well as the Cordillera de la Costa, the Cordillera de Mérida, and the Serranía de Perijá. With nine of the 14 Venezuelan species occurring in the Guiana region (with the highlands and the surrounding lowlands), that region constitutes a minor center of diversity for sect. *Pachyneurium*. If the non-Venezuelan parts of the Guianas are included, three more endemic species would be added, *A. cowanii*, *A. lanjouwii*, and *A. maguirei*. Seven species with eight taxa occur in the far south of Venezuela in the Guiana Highlands and the adjacent northern Amazon basin. These are *A. bonplandii* subsp. *bondplandii*, *A. bonplandii* subsp. *cuatrecasii*, *A. cataniapoense*, *A. guanchezii*, *A. iramirezae*, *A. vinillense*, *A. wurdackii*, and *A. xanthoneurum*. One additional species which ranges into the Amazon basin is *A. jenmanii*. This species has an unusual distribution in that it also occurs in Trinidad and the eastern end of the Cordillera de la Costa bordering the Caribbean, then ranges east and south through the Guiana lowlands to Amapá State in Brazil. It is the only species besides *A. fendleri* that enters the Amazon basin and also occurs primarily outside of the Amazon basin.

Five taxa, *A. bonplandii* subsp. *guayanum*, *A. iramirezae*, *A. vinillense*, *A. wurdackii*, and *A. xanthoneurum*, are restricted to the Guiana Highlands. One species, *A. wagenerianum*, is restricted to the Cordillera de la Costa in northern Venezuela. Two additional species, *A. crassinervium* and *A. fendleri*, inhabit the Cordillera de la Costa but also

range throughout the Cordillera de Mérida and into Colombia. In addition, disjunct populations of *A. fendleri* occur in the western Cordillera and the Chocó of Colombia as well as in Panama. *Anthurium cubense* is restricted to the northwestern part of the country in the Serranía de Perijá west of Lake Maracaibo (Zulia State) and to the east in Falcón. This species inhabits generally drier areas around the western and southern margins of the Caribbean.

Venezuela has more than one-third of its species endemic, including *A. guanchezii*, *A. iramirezae*, *A. vinillense*, *A. wurdackii*, and *A. xanthoneurum* in the Guiana region. *Anthurium wagenerianum* is essentially endemic, being otherwise known only from Curaçao.

The Guianas. Like much of eastern South America, the Guianas are relatively low in species diversity. The region has only five known species of sect. *Pachyneurium*, with a sixth species purportedly described from the region but never found (*A. martianum*). Only one of the five species, *A. jenmanii*, occurs in the lowlands ranging from Venezuela, down the coast of the Guianas to Amapá in Brazil. It is the only species known for certain from French Guiana. The highland species are *A. bonplandii* subsp. *guayanum*, known from Surinam; *A. cowanii*, endemic to Guyana; *A. lanjouwii* and *A. maguirei*, endemic to Surinam.

Despite the low number of species in the Guiana region, the rate of endemism is high, with three of the five species endemic. If *A. martianum* (purportedly from Surinam) really did come from Guyana, the rate of endemism for this area would be higher still.

West Indies. Section *Pachyneurium* in the West Indies is restricted to the Greater Antilles and to some of the smaller islands in the region, notably the Virgin Islands. Only three species occur in the Lesser Antilles, *A. jenmanii* on Trinidad and Tobago, and *A. crassinervium* and *A. wagenerianum* on Curaçao. A sect. *Pachyneurium* look-alike, *A. hookeri*, occurs more widely in the Lesser Antilles, as far north as Montserrat. Cuba, the largest island of the Greater Antilles, has only two species of *Pachyneurium*, *A. cubense* and *A. venosum*. *Anthurium cubense* also ranges to Central and South America, while *A. venosum* possibly ranges to Jamaica (see discussion under *A. venosum* for details of differences of Jamaican material). Hispaniola has but a single species, *A. crenatum*. This is the most wide-ranging species of sect. *Pachyneurium* endemic to the West Indies, ranging from Hispaniola to Puerto Rico and the Virgin Islands. Puerto Rico has one species, *A. crenatum*, and St. John, Virgin Islands has one endemic species, *A. selloum*.

While three of the six West Indian species of *Pachyneurium* are endemic to the West Indies, only *A. selloum* is endemic to a particular island.

CENTERS OF ENDEMISM (General Comments)

It is illustrative to look at the distribution of endemic species, since this does not always coincide with the centers of maximum species diversity for sect. *Pachyneurium*. Although Ecuador and Peru again come out on top with 23 and 13 endemic taxa, respectively, several countries have between ¼ and ¾ of their taxa endemic. Mexico has 5 of its 7 taxa endemic, while Costa Rica has 7 of 23, Panama 5 of 23, Colombia 6 of 24, Venezuela 5 of 14, Guyana 2 of 3, Brazil 6 of 18, and the West Indies 3 of 6. In contrast, there are no endemic species in Central America outside of Costa Rica. These patterns in Central America are reflected in the genus as a whole (Croat, 1987), where Mexico as well as Panama and Costa Rica are shown to be major centers of endemism.

There are 79 taxa endemic to individual countries throughout the range of sect. *Pachyneurium*. Although the rate of endemism, country by country, is not a particularly useful index, since some countries, e.g., Brazil, are vastly larger than others, such as Ecuador, Costa Rica, or Panama, the overall rate of endemism for sect. *Pachyneurium* is relatively high. If we consider all the countries in Central America and South America as well as Cuba, Hispaniola, and Puerto Rico, there are an average of 3.7 species endemic for each. Central America considered alone has 19 endemics, while South America has 59 and the West Indies has 3.

Endemism, it would appear, is no indicator of the center of origin of sect. *Pachyneurium*, since endemics appear throughout the range of the section. Rather, endemism in the section appears to be more a matter of isolation, since for the most part the endemics are most common in areas where the relief is broken, or where there are isolated intermountain valleys, such as in the Andes of western South America or in the Guiana Highlands. Species in series *Multinervia*, which is particularly high in endemics (with all but 5 of 16 taxa endemic to Ecuador), reflects this well. Most occur in valleys on both slopes of the Continental Divide, where the degree of isolation tends to be high. Other causes for endemism may stem from isolation due to the discontinuous nature of life zones. For example, the Caribbean slope of Costa Rica and Panama is

broken by discontinuous areas of tropical moist forest, premontane wet forest and tropical wet forest. *Anthurium prolatum*, for instance, is primarily restricted to areas of tropical wet forest in northeastern Costa Rica, while *A. concolor* is known principally from another wet area further to the east in Panama. These two regions are interrupted by a broad area of tropical moist forest in northeastern Panama and southeastern Costa Rica.

Relatively few species inhabiting upland regions are very widespread, but some, such as *A. dombeyanum*, are moderately wide-ranging, extending from southern Peru to northern Ecuador. Other wide-ranging species occur mostly from near sea level to middle elevations. Among such species are: *A. schlechtendalii* (Mexico to Nicaragua), *A. salviniae* (Mexico to south central Colombia), *A. fendleri* (Amazonian Colombia to Panama), and *A. cubense* (Cuba to Central America and northern South America).

In contrast, the lowland species, such as those inhabiting the Amazon basin, are much more widespread, e.g., *A. atropurpureum*, *A. bonplandii*, *A. ernestii*, *A. plowmanii*, and *A. uleanum*.

Endemic *Anthurium* species by region are summarized in the following list:

West Indies (3)
- *crenatum*
- *selloum*
- *venosum*

Mexico and Central America (excluding Costa Rica & Panama) (6)
- *halmoorei*
- *machetioides*
- *nizandense*
- *salvadorense*
- *sarukhanianum*
- *schlechtendalii*

Costa Rica and Panama* (25)
- *acutifolium*
- *bradeanum*
- *brenesii*
- *colonicum*
- *consorbrinum*
- *cotobrusii*
- *eximium*
- *fatoense*
- *hammelii*
- *luteynii*
- *nervatum*
- *oerstedianum*
- *prolatum*
- *protensum*
- *pseudospectabile*
- *purpureospathum*
- *ranchoanum*
- *schottianum*
- *seibertii*
- *spathiphyllum*
- *spectabile*
- *standleyi*
- *upalaense*
- *validifolium*
- *watermaliense*

Northern South America (extra-Amazon) (8)
- *anorianum*
- *caucavallense*
- *crassinervium*
- *glaucospadix*
- *jenmanii*
- *johnsoniae*
- *wagenerianum*
- *fendleri***

Coastal lowlands of western South America (5)
- *asplundii*
- *barclayanum*
- *linguifolium*
- *manabianum*
- *simpsonii*

Andes, western slope (15)
- *acutissimum*
- *angustilaminatum*
- *bucayanum*
- *campii*
- *carchiense*
- *holmnielsenii*
- *lennartii*
- *leonianum*
- *napaeum*
- *narinoense*
- *obscurinervium*
- *oxyphyllum*
- *palenquense*
- *pallatangense*
- *sparreorum*

Andes, eastern slope (21)
- *basirotundum*
- *bushii*
- *curtispadix*
- *dombeyanum*
- *fasciale*
- *harliangianum*
- *knappiae*
- *latissimum*
- *llewelynii*
- *manuanum*
- *ottonis*
- *pachylaminum*
- *paraguayense*
  - var. *coroicoanum*
- *penningtonii*
- *reflexinervium*
- *remotigeniculatum*
- *santiagoense*
- *solomonii*
- *soukupii*
- *tarapotense*
- *tenaense*

* Some extending into the southeastern part of Nicaragua.
** Rare in Panama.
*** Counts refer to species, not taxa, i.e., not including varieties and subspecies except where split into separate endemic regions.

Guiana Highlands (8)
bonplandii subsp. *guayanum*
cowanii
iramirezae
lanjouwii
maguirei
vinillense
wurdackii
xanthoneurum

Amazon basin (17)
atropurpureum
bonplandii
***subsp. *bonplandii*
subsp. *cuatrecasii*
cataniapoense
ernestii
galactospadix
guanchezii
krukovii
loretense
oxycarpum
pendulifolium
plowmanii
pranceanum
superbum
uleanum
vaupesianum
willifordii

Brazilian Highlands of south-central and eastern Brazil (2)
affine
lindmanianum

Southeastern Brazil (2)
coriaceum
solitarium

Temperate and subtropical South America (1)
paraguayense var. *paraguayense*

Species not included in areas of endemism (4)
concolor, Panama to northern Colombia
cubense, circum-Caribbean
martianum, location not known
salviniae, Mexico to northern Colombia

ABUNDANCE

Despite the fact that *Pachyneurium* species are not very wide-ranging in general (see section on Geographical Distribution), species are commonly quite abundant on a local basis. For example, *A. atropurpureum* var. *arenicola* is rare in Brazil in Rondônia, near an extreme of its range, but abundant locally around Iquitos. Species such as *A. anorianum*, *A. pachylaminum*, *A. penningtonii*, *A. pseudospectabile*, *A. reflexinervium*, *A. salvadorense*, *A. schottianum*, *A. seibertii*, *A. standleyi*, and others that have relatively narrow ranges are nevertheless often very abundant locally.

In an area where any species occurs the plants commonly dominate the local epiphytic landscape, due to their generally large size, conspicuous habit, and ability to adapt to a wide variety of local conditions. Typically, epiphytic species adapt readily to other niches such as on rocks or limestone outcrops within a forest understory or on steep road cuts or stream banks. While quite at home in the understory of a dense forest, plants there are usually much less numerous. While being able to withstand low light levels indefinitely, plants react quickly to openings that increase light levels. Clearing edges eventually become favorite sites for *Pachyneurium* species. Their ability to survive in the sunnier habitats, and their avian fruit-dispersal agents, always more prevalent in such habitats, are no doubt chiefly responsible for their much greater success in such open habitats. A single large plant that has been pollinated may produce thousands of seeds, many of which are scattered locally. Seedlings are in general quite successful, and a local population may soon consist of hundreds of plants, especially in disturbed sites. Predation by phytophagous insects seems to be only a minor problem, perhaps due to the tough epidermis and the seemingly lower number of phytophagous insects in the seasonally dry areas where *Pachyneurium* is most prevalent. The ability to survive in low-light conditions, as well as in high illumination with limited moisture, make *Pachyneurium* species preadapted for many abuses they might receive under cultivation. Indeed, some species, such as *A. schlechtendalii* are very common in cultivation. Their adaptations for conditions of seasonal drought apparently make them somewhat cold-resistant as well. A number of species cultivated in south Florida and in southern California are capable of surviving night temperatures at or near freezing.

INTERSPECIFIC RELATIONSHIPS

Although mention has already been made of a high degree of endemism within sect. *Pachyneurium* and the great dissimilarity between Central and South American species in the section, there are several important groups of related species. These groups are outlined below:

Group 1: *A. anorianum*
A. concolor
A. crassinervium
A. crenatum
A. cubense
A. halmoorei
A. machetioides
A. nizandense
A. purpureospathum
A. salvadorense
A. salviniae
A. schlechtendalii
A. upalaense

Occurring in Central America and mostly northern, extra-Amazonian South America, this group of species consists of typical members of series *Pachyneurium*, mostly with red fruits, typical rosulate habit, D-shaped petioles, often with abaxial ribbing. Although breeding studies between some of the Central and South American species have shown little relationship, all of the species listed here have probably have had at least ancient contact with one another. There are no mountain ranges separating these species and, indeed, two range throughout much of the area, namely *A. salviniae* and *A. cubense*.

Group 2: *A. brenesii*
A. colonicum
A. cotobrusii
A. hammelii
A. luteynii
A. nervatum
A. prolatum
A. protensum
A. pseudospectabile
A. ranchoanum
A. seibertii
A. spectabile
A. standleyi
A. validifolium

This group, known almost exclusively from Costa Rica and Panama (a few lap over into the wet southeastern corner of Nicaragua), is characterized by its orange fruits. Many members of the group have cordate to subcordate, greenish-drying blades (in contrast to typical *Pachyneurium*), frequently with the collective veins arising from near the base.

Group 3: *A. acutifolium*
A. bradeanum
A. consobrinum
A. eximium
A. spathiphyllum

This small group is characterized by moderately thin, greenish-drying leaves, thin cataphylls which often persist intact, and less conspicuously colorful fruits, generally yellowish, greenish, or whitish (though tipped with red or purple in *A. consobrinum* and solid red in *A. eximium*). Fruits are not yet known for *A. spathiphyllum*, but it is believed to be closely related to *A. bradeanum*, which has white fruits. In addition, all but *A. acutifolium* have cylindroid or clavate spadices.

Anthurium schottianum and *A. oerstedianum* stand alone in Central America, seemingly not being closely related to any other species. The former is unusual in having a thin, cordate blade with free-ending basal veins and in its markedly seasonal flowering behavior (several inflorescences apparently synchronize to emerge at about the same time). While berry color is described as pinkish, darker toward the apex and possibly red, the species is not at all related to other red-fruited species in Central or South America. *Anthurium oerstedianum* is unknown as to fruit color, but with its strange leaf blades with the geniculum situated at the middle of the petiole, it seems to be unrelated to any other Central American species.

Group 4: *A. atropurpureum*
A. bonplandii
A. cowanii
A. fendleri
A. guanchezii
A. iramirezae
A. jenmanii
A. krukovii
A. lanjouwii
A. lindmanianum
A. maguirei
A. pachylaminum
A. pendulifolium
A. pranceanum
A. remotigeniculatum
A. vinillense
A. wurdackii
A. xanthoneurum

Basically a group from the Guianas, lowland Amazonia and the Brazilian highlands, this group is characterized by purple fruits and the tendency to occur on granitic outcrops or on sandy soil or in areas of extensive white sand deposits. Many have pustules or glandular dots on the leaves, thin spathes, and minutely papillate tepals.

Group 5: *A. asplundii*
A. bushii
A. cataniapoense

A. harlingianum
A. loretense
A. vaupesianum

A closely related group of species with densely rosulate, mostly large, short-petiolate leaves, thin spathes, and long-tapered purplish spadices with minutely papillate tepals and purple fruits.

Group 6: *A. bucayanum*
A. campii
A. lennartii
A. manabianum
A. sparreorum

These species all occur on the Pacific slope of the Andes in Ecuador and have large, mostly green-drying leaves with short petioles, numerous primary lateral veins and a collective vein arising from near the base.

Group 7: *A. curtispadix*
A. ernestii
A. galactospadix
A. manuanum
A. tenaense
A. uleanum

A closely related group from western Amazonia, mostly at low elevations, frequently with minutely papillate tepals which dry with a crustose, frostlike appearance (most noticeable in *A. uleanum*) and mostly short petioles and peduncles.

Group 8: *A caucavallense*
A. dombeyanum
A. glaucospadix
A. latissimum
A. leonianum
A. llewelynii
A. paraguayense
A. reflexinervium
A. solomonii
A. tarapotense

These highland species with purple fruits share in common a tight rosulate habit, mostly short, D-shaped petioles, thick blades, and purplish spadices. Many have a tendency for the lowermost primary lateral veins to extend out from the midrib at a broad angle (most pronounced in *A. paraguayense* var. *coroicoanum*, *A. latissimum*, and *A. reflexinervium*). *Anthurium johnsoniae* perhaps also belongs here. Occurring in the mountains above Santa Marta in northern Colombia, this species would be unusual for the group in having orange fruits, but it shares many features in common with *A. caucavallense*, especially the broadly spreading primary lateral veins. Perhaps it is the result of an ancient hybridization between *A. crassinervium* (currently occurring in close proximity) and *A. caucavallense*, as it shares characteristics in common with both of these species.

Group 9: *A. superbum*
A. willifordii

This strange pair of species, no doubt closely related, is characterized by quilted leaves, sometimes tinged purplish or reddish below, short-pedunculate, stubby cylindroid spadices with many minute flowers per spiral, and lavender or magenta, often bicolorous fruits.

Group 10: *A. barclayanum*
A. linguifolium
A. simpsonii

These purple-fruited species all occur along the Pacific coast of South America in Peru and Ecuador, in generally arid areas (less so for *A. simpsonii*).

Group 11: *A. acutissimum*
A. angustilaminatum
A. carchiense
A. fasciale
A. holmnielsenii
A. narinoense
A. oxyphyllum

Most of these Andean species occur on the Pacific slope (*A. fasciale* occurs on the Atlantic slope) of Ecuador and have orange, red, or red-orange fruits. All are members of series *Multinervia* with oblong to oblong-elliptic blades and close primary lateral veins.

Group 12: *A. napaeum*
A. obscurinervium
A. ottonis
A. palaenquense
A. pallatangense
A. penningtonii
A. santiagoense
A. soukupii

All members of series *Multinervia*, these species have purple fruits or are most closely related to other members of series *Multinervia* with purple fruits. Many tend to have triangular petioles, sometimes sharply so.

Group 13: *A. knappiae*
A. oxycarpum

This pair of species, though not close geograph-

ically, seem very closely related. Both share moderately thin, veiny blades with the collective veins arising from the base. Though *A. oxycarpum* is moderately widespread in the Amazon lowlands and on the eastern slopes of the Andes, *A. knappiae* occurs only on the eastern slopes of the Andes in San Martín Department.

Among the South American species that appear to have no close relatives are *A. affine*, *A. coriaceum*, *A. plowmanii*, and *A. solitarium*.

Anthurium affine sometimes resembles *A. lindmanianum*, a species discussed above as having affinity with a relatively large group of lowland Amazonian species common on rocks and sand. *Anthurium affine*, like *A. lindmanianum*, is relatively isolated in the central highlands of Brazil and differs from all other species in the above group by its unusual spadix, which is generally broadest toward the apex.

Restricted to southeastern Brazil and in an area where no other *Pachyneurium* species occur, are two species, *A. coriaceum* and *A. solitarium*. They are apparently totally unrelated to each other.

Anthurium plowmanii appears to be quite anomalous, with its petioles narrowly sulcate with blunt margins adaxially and a spadix longer than the peduncle.

Aside from *A. crenatum* and *A. cubense*, which show relationships to other *Pachyneurium* species from Central America and northern South America, the other West Indian species show no close relationship with other members of the section. *Anthurium venosum*, endemic to Cuba, shows no features in common with any other species, and *A. selloum* (discussed elsewhere as a possible hybrid) likewise is unique among the West Indian species.

TAXONOMIC TREATMENT

Anthurium Schott, Wiener Z. Kunst 828. 1829 (3rd Quart.). LECTOTYPE: *Anthurium acaule* (Jacq.) Schott. *Pothos acaulis* Jacq., Enum. Syst. Pl. 31. 1760 (vide ING).

Herbs, usually epiphytic, less often terrestrial or lithophytic, the growth habit monophyllous or rarely polyphyllous sympodial; petioles variously shaped, usually conspicuously geniculate at apex; leaf blades simple to palmately divided or compound with the lesser veins reticulate; inflorescence terminal (but appearing axillary), one per leaf; spathe free, persistent; spadix uniformly tapered; flowers perfect, densely arranged in spirals, tepals 4, cucullate at apex and usually overtopping pistils; stamens 4; pollen globose, forate or rarely (sect. *Polyphyllium*) inaperturate, the exine basically reticulate; ovary 2-locular, with 1 or 2 ovules per cell, rarely 3 or more; fruit a berry.

Anthurium sect. **Pachyneurium** Schott, Prodr. 466. 1860. *Pothos crenata* L. Sp. Pl. Ed. 2: 1373. 1763. TYPE SPECIES: *Anthurium crenatum* (L.) Kunth, Enum. Pl. 3: 75. 1841.

grex *Oxycarpium* Schott, Prodr. 450–451. 1860. TYPE SPECIES: *Anthurium oxycarpum* Poeppig in Poeppig & Endl. Nov. Gen & Sp. 3: 83. T. 293.f.B. 1845

Epiphytic, terrestrial or lithophytic herbs, often large; stems usually short, with short internodes; roots numerous, usually dense; cataphylls usually straight, lanceolate, rarely hooked or cucullate, usually quickly weathering and persisting as fibers. *Leaves* rosulate; petioles mostly short and about ⅓ or less as long as blades, sometimes elongate but rarely as long as blades, stiff to flexible, weakly sheathed near base, rarely throughout much of length, geniculate at apex, the cross-sectional shape various, often D-shaped, rarely terete, sometimes with ribs abaxially, often broadly sulcate with raised margins and sometimes also a medial rib adaxially; blades coriaceous to subcoriaceous, rarely thinner, mostly oblanceolate to elliptic, rarely subcordate to cordate or with conspicuous posterior lobes. *Inflorescence* erect to pendent; peduncle usually terete, short to elongate; spathe usually spreading to reflexed, sometimes recurled, rarely erect or hooding spadix, green, sometimes tinged purple or reddish (especially adaxially); spadix tapered to cylindroid, rarely clavate, usually sessile, green to purplish or reddish, sometimes whitish; flowers truncate and rhombic to square in outline at apex; tepals usually matte to weakly glossy, sometimes with nectar droplets, the outer margin 2–4-sided, the inner margin mostly broadly rounded; stigma sessile, slitlike, lined with papillae, or sometimes brushlike; stamens with filaments rarely exserted, anthers usually clustered around and held tightly over the pistils, rarely long-exserted; pollen yellow or orange, rarely purplish at anther-dehiscence, quickly fading to pale yellow or white. *Infructescence* mostly pendent, occasionally erect; berries mostly obovoid, sometimes somewhat ellipsoid, acute to rounded or truncate at apex, exserted and held by tepalar threads at maturity, variously colored, mostly purplish, red, or orange, rarely yellow or white, 1–2-seeded; mesocarp usually gelatinous, rarely pulpy; seeds mostly oblong-elliptic, usually with a gelatinous appendage.

KEY TO SERIES OF *ANTHURIUM* SECTION *PACHYNEURIUM*

Blades usually oblanceolate to oblanceolate-elliptic, rarely oblong-elliptic or ovate to ovate-cordate, usually drying brown, reddish brown, greenish brown, or blackened, rarely greenish or yellowish green; primary lateral veins usually widely spaced and stout (generally more than 3 cm apart), much more conspicuous than the interprimary veins (the latter usually lacking); fruits usually red or purple to purplish in South America, often orange in Costa Rica and Panama; found throughout the range of the section ..... series *Pachyneurium*

Blades usually oblong-elliptic to oblong-oblanceolate or elliptic, rarely oblanceolate, usually drying green to yellow-green; primary lateral veins usually moderately weak, usually closely spaced (generally less than 3 cm apart); interprimary veins usually many, these almost as conspicuous as the primary lateral veins; fruits mostly orange, sometimes purple; mostly endemic to Ecuador, also Nariño, Colombia to Bolivia ..... series *Multinervia*

Anthurium series **Pachyneurium** (Schott) Croat, comb. nov. *Anthurium* grex *Pachyneurium* Schott Prodr. 466. 1860.

Anthurium series **Multinervia** Croat, ser. nov. TYPE: *Anthurium napaeum* Engl.

Differt a serie *Pachyneurium* laminae in sicco viridibus cum nervis primaries lateralibus vix conspicuioribus nervis interprimaries.

For an indication of species in series *Multinervia* see the species preceded by an asterisk in Appendix 3.

KEY TO SPECIES OF *ANTHURIUM* SECTION *PACHYNEURIUM*

1a. Species of Mexico, Central America, Panama, and West Indies.
- 2a. Blades ovate to narrowly ovate or oblong-ovate, sagittate to cordate, subcordate or hastate at base; mostly less than 2× longer than wide (to 3× longer than wide in *A. selloum* from West Indies); the posterior lobes usually more than ¼ as long as the anterior lobes.
  - 3a. Spadix with pistils early emergent, well above the tepals at anthesis, giving the spadix a rough appearance; stamens often long-exserted and remaining exserted after anthesis.
    - 4a. Blades truncate to subcordate at base, the posterior lobes about as long as wide; spathe margin markedly undulate; Central Panama; 0–1,150 m ..... *A. colonicum* K. Krause
    - 4b. Blades deeply cordate-sagittate to hastate at base, the posterior lobes 1.5–3.0× longer than wide; spathe with margins ± flat and straight; Costa Rica to Colombia; 0–2,400 m ..... *A. watermaliense* hort. ex Bailey & Nash
  - 3b. Spadix with pistils held mostly below tepals at anthesis; stamens scarcely exserted and retracted to level of tepals after anthesis.
    - 5a. Blades with collective veins arising from one of the basal veins (rarely from one of the lowermost primary lateral veins).
      - 6a. Blades with the basal veins all free to the base; sinus narrowly triangular to closed; less than 300 m.
        - 7a. Blades 44–100 cm long; primary lateral veins 9–20 pairs; southeastern Costa Rica; less than 100 m ..... *A. schottianum* Croat & R. A. Baker
        - 7b. Blades 17–46 cm long; primary lateral veins 5–9 pairs Cuba; less than 300 m ..... *A. venosum* Griseb.
      - 6b. Blades coriaceous, at least the lowermost pairs of basal veins coalesced to form a marginal posterior rib; sinus arcuate to parabolic or obovate to clavate; Costa Rica and Panama; above 500 m or St. John, Virgin Islands, at less than 300 m.
        - 8a. Blades with 4–9 pairs of primary lateral veins; berries not early emergent, rounded at apex.
          - 9a. Inflorescence nodding before anthesis; spathe hooding spadix at anthesis; spadix cylindrical less than 6× longer than broad ..... *A. ranchoanum* Engl.
          - 9b. Inflorescence erect before anthesis; spathe spreading-recurved, never hooding spadix at anthesis; spadix markedly tapered, 10–20× longer than broad; 600–1,850 m ..... *A. cotobrusii* Croat & R. A. Baker
        - 8b. Blades with 19–25 pairs of primary lateral veins; berries early emergent, acute at apex ..... *A. nervatum* Croat
    - 5b. Blades with collective veins arising from one of the primary lateral veins in the upper ½ of the blade.
      - 10a. Blades prominently lobed at base, the sinus hippocrepiform or spathulate to obovate with the lobes sometimes overlapping; Costa Rica and Panama.
        - 11a. Blades usually less than 50 cm long, broadest at or near the base; sinus arcuate to parabolic or hippocrepiform; spadix usually less than 20× longer than broad; Costa Rica to Panama; 600–1,850 m ..... *A. cotobrusii* Croat & R. A. Baker
        - 11b. Blades usually more than 50 cm long, broadest at point of petiole attachment; sinus clavate to obovate; spadix usually more than 20× as long as broad; Costa Rica; 200–1,600 m ..... *A. standleyi* Croat & R. A. Baker
      - 10b. Blades merely subcordate to almost truncate at base (rarely more deeply lobed); sinus triangular arcuate to arcuate with decurrent petiole, (rarely subparabolic in *A. selloum*), lobes never even approaching overlap; West Indies (St. John, Virgin Islands); less than 300 m ..... *A. selloum* K. Koch
- 2b. Blades elongate, mostly 3 or more × longer than wide, mostly oblong-elliptic to obovate or oblanceolate, only rarely subcordate at base (if so, the posterior lobes less than $\frac{1}{10}$ as long as anterior lobes).
  - 12a. Collective veins arising from the lower ¼ of the blade, often from near the base.
    - 13a. Spadix purplish or brownish at anthesis.
      - 14a. Primary lateral veins prominently sunken above, prominently raised beneath.
        - 15a. Petioles subquadrangular, 3–5-ribbed adaxially; Panama and Costa Rica in Cordillera de Talamanca; 1,300–2,000 m ..... *A. seibertii* Croat & R. A. Baker
        - 15b. Petioles terete or subterete, rounded or bluntly angulate adaxially.
          - 16a. Blades more than 83 cm long; spadix 30–75× longer than broad, to 60 cm long, the fruiting spadix more than 30 cm long; Atlantic slope of Costa Rica and in western Panama; 200–600 m ..... *A. prolatum* Croat & R. A. Baker
          - 16b. Blades less than 80 cm long; spadix less than 20× longer than broad at anthesis, to 20 cm long, the fruiting spadix usually less than 25 cm long; above 900 m.

17a. Leaf blades usually more than 50 cm long, usually ± pendent; spathe oblong-lanceolate to lanceolate; spadix usually more than 9 cm long; Costa Rica and Panama; 635–2,700 m ..... *A. protensum* Schott subsp. *protensum*

17b. Leaf blades usually less than 50 cm long; usually erect; spathe ovate to broadly lanceolate; spadix usually less than 6.5 cm long; mostly western Panama; 1,100–2,000 m ..... *A. protensum* Schott subsp. *arcuatum* Croat

14b. Primary lateral veins and collective veins not prominently sunken above, slightly raised beneath.

18a. Blades oblong, broadest midway; primary lateral veins 13–16 pairs, drying inconspicuous, scarcely more conspicuous than interprimary veins; petioles terete; spathe ovate to ovate-elliptic, hooding spadix; Cordillera Tilarán and Cordillera Central in northern Costa Rica ..... *A. brenesii* Croat & R. A. Baker

18b. Blades oblanceolate to oblong-oblanceolate, broadest well above middle; primary lateral veins 9–14 pairs, conspicuous, much more prominent than the interprimary veins; petioles subquadrangular to trapezoidal; spathe lanceolate, spreading, not hooding spadix; western Mexico ..... *A. schlechtendalii* Kunth subsp. *jimenezii* (Matuda) Croat

13b. Spadix greenish to green or whitish at anthesis.

19a. Petiole with geniculum situated at least 7 cm below base of blade; Pacific slope of southwestern Costa Rica; 300–1,300 m . *A. oerstedianum* Schott

19b. Petiole with geniculum immediately subtending leaf blade.

20a. Plants pendent epiphytes; blades usually more than 1 m long and 25 cm wide.

21a. Petioles subterete, rarely bluntly 4-sided; blades 6–8× longer than wide, matte to semiglossy on upper surface; western Panama; 1,250–1,500 m ..... *A pseudospectabile* Croat

21b. Petioles sharply quadrangular; blades 2.5–4× longer than wide, semiglossy to glossy on upper surface; Nicaragua and Costa Rica; 300–1,300 m ..... *A. spectabile* Schott

20b. Plants erect, epiphytic or terrestrial; blades usually less than 80 cm long and less than 14 cm wide (sometimes wider in *A. jimenezii* from Pacific slope of Mexico).

22a. Spadix long-tapered, greenish; petioles less than 7 cm long, rounded abaxially; endemic to Central Mexico in Oaxaca on Atlantic slope; 200–1,200 m ..... *A. machetioides* Matuda

22b. Spadix oblong to clavate, scarcely or not at all tapered, cream to white or pale yellow; petioles more than 7 cm long, rounded to 3-ribbed abaxially; Nicaragua and Costa Rica.

23a. Petioles longer than the blades; spathe dark reddish purple, nearly round, ca. 7 cm wide; western Panama; 1,675 m ..... *A. hammelii* Croat

23b. Petioles 1/5–1/8 as long as blades; spathe green, at most lanceolate-ovate, less than 3 cm wide; Nicaragua to Panama; 0–1,600 m.

24a. Cataphylls persisting intact; petioles rounded to 3-ribbed abaxially; blades with raphide cells visible (at least when dried); primary lateral veins 10–12 pairs, weakly sunken on upper surface; spathe lanceolate-ovate, reflexed; spadix creamy white, cylindroid to clavate, not tapered toward apex, held at ca. 90° angle to peduncle; Pacific slope of southwestern Costa Rica; 0–1,600 m ..... *A. eximium* Engl.

24b. Cataphylls weathering to fibers; petioles triangular or sharply 3–5-ribbed abaxially; blades with raphide cells not visible; primary lateral veins 20–30 pairs, prominently sunken on upper surface; spathe lanceolate to broadly lanceolate, erect and cucullate; spadix pale yellow to creamy white, erect or suberect, slightly tapered toward apex, held at ca. 180° angle to peduncle; Nicaragua to Panama; 0–380 m ..... *A. spathiphyllum* N. E. Br.

12b. Collective veins arising from the upper ¾ of the blade, mostly from above the middle or lacking.

25a. Spadix purplish or rarely reddish at anthesis (mostly lavender to violet-purple).

26a. Blades with reticulate veins prominulous on both surfaces even when fresh, drying prominently raised; West Indies (Dominican Republic, Puerto Rico, and Virgin Islands) ..... *A. crenatum* (L.) Kunth

26b. Blades with reticulate veins on fresh leaves either obscure or sunken above, flat to weakly raised below, drying weakly raised; Central America and northern South America (*A. cubense* also from Cuba).

27a. Peduncle usually shorter than petiole, never more than twice as long as petiole, usually less than twice as long as spadix (rarely somewhat more than twice as long as spadix).

28a. Petioles sharply to bluntly quadrangular or D-shaped, rounded or usually 1–3-ribbed abaxially, spadix dark violet-purple at anthesis; Panama, Atlantic Coast to Continental Divide in wetter parts of tropical moist forest and premontane wet forest, sea level to 1,500 m ..... *A. purpureospathum* Croat

28b. Petioles subterete to obscurely quadrangular, usually rounded adaxially; spadix whitish to lavender at anthesis; Cuba, Yucatán to Panama, Colombia, and Venezuela in tropical dry forest and drier parts of tropical moist and premontane wet forest life zones; 100–700 m ..... *A. cubense* Engl.

27b. Peduncle mostly 2 or more × longer than petiole, usually 2 or more × longer than spadix.

29a. Petioles either subquandrangular in cross section, or 3- or more-ribbed abaxially or both.

30a. Petiole lacking abaxial ribs, eastern Costa Rica and western Panama; 1,200–2,300 m ..... *A. validifolium* K. Krause

30b. Petiole with abaxial ribs.

31a. Spathe dark purple, coriaceous, cucullate and hooding spadix at anthesis; spadix broadest at about lower ⅓; Panama, tropical wet and premontane rainforest life zones; 530–1,350 m ..... *A. luteynii* Croat

31b. Spathe green (sometimes tinged purplish) reflexed, never hooding spadix.

32a. Spadix cylindrical, 7–20× longer than broad at anthesis; tepals bearing conspicuous droplets over their surface at anthesis; spathe oblong-ovate to oblong-elliptic, usually less than 4× longer than broad at anthesis; blades drying brown; Atlantic Coast of Panama to Colombia; less than 100 m ..... *A. concolor* K. Krause

32b. Spadix long-tapered, usually more than 20× longer than broad at anthesis; tepals lacking droplets (except in *A. upalaense* after 2 or more stamens have emerged); spathes mostly lanceolate, 5 or more × longer than broad at anthesis.

33a. Petioles subquandrangular, prominently 3–5-ribbed abaxially; blades acute at base, drying brown to gray-green on lower surface; cataphylls coriaceous, persisting intact; spathe moderately thick, persisting intact; Atlantic slope of Nicaragua and Costa Rica; mostly 0–700 m (rarely to 1,300 m ..... *A. upalaense* Croat & R. A. Baker

33b. Petioles D-shaped, rounded to subtriangular, weakly 1–5-ribbed adaxially; blades usually obtuse to rounded at base; drying pale yellowish green on lower surface; cataphylls moderately thin, soon weathering to semi-intact condition or to fibers or deciduous; spathe thin, soon drying and weathering; principally northern South America but extending into Central Panama; mostly 0–1,000 m ..... *A. fendleri* Schott

29b. Petioles more or less D-shaped in cross section, rounded and unribbed abaxially.

34a. Spadix subcylindroid, less than 10 cm long; pistils sharply pointed, early emergent; tepals greenish white, turning pinkish tan ..... *A. consobrinum* Schott

34b. Spadix long-tapered, greater than 10 cm; pistils rounded at apex, not at all early emergent; tepals maroon or green, soon lavender.

35a. Spadix dark maroon, not at all glaucous; cataphylls lanceolate, the young leaves emerging straight from cataphyll, lacking circinnate vernation (not rolled lengthwise); berries purplish, sometimes white at base; Trinidad, northeastern South America to Brazil (Amapá) ..... *A. jenmanii* Engl.

35b. Spadix pale green when young, soon lavender, weakly glaucous; cataphylls cucullate, fist-shaped, the leaves unrolling lengthwise; berries red; Mexico to Colombia; 0–1,600 m ..... *A. salviniae* Hemsley

25b. Spadix green, greenish, white, yellow, or yellow-green at anthesis.

36a. Petioles subquadrangular or trapezoidal in cross section.

37a. Spathe narrowly to broadly ovate to elliptic, less than 3.5× longer than broad, held erect, enshrouding or hooding spadix (except for *A. halmoorei*).

38a. Spadix clavate, broadest somewhat above the middle, directed at ca. 90° angle from peduncle; spathe boat-shaped and hooding the spadix at anthesis; berries greenish yellow to white; petioles sharply quadrangular with raised edges, usually sharply 3-angular abaxially; Atlantic slope, Nicaragua to Panama; 0–450 m, rarely to 800 m ..... *A. bradeanum* Croat & Grayum

38b. Spadix tapered toward the apex, broadest at the base, held erect or suberect; spathe spreading or erect and enshrouding (but not hooding) spadix at anthesis; berries yellow or red; petioles bluntly quadrangular.
39a. Spathe stiffly erect and enshrouding spadix; berries orange-red; El Salvador and Guatemala; Pacific slope; 500–800 m ..... *A. salvadorense* Croat
39b. Spathe spreading, never enshrouding spadix; berries pale yellow; western Mexico, Nayarit, Jalisco, and Michoacán; 450–1,000 m ..... *A. halmoorei* Croat

37b. Spathe lanceolate to narrowly triangular, usually more than 3.5× longer than wide (sometimes to 3× longer than wide for *A. nizandense*).
40a. Blades elliptic to obovate-elliptic, less than 3× longer than wide, widest at about the middle; roots mostly thick, to 1 cm diam.; Pacific slope of Mexico (Guerrero and Oaxaca); to 850 m ..... *A. nizandense* Matuda
40b. Blades oblanceolate to obovate, usually more than 3.5× longer than wide, always widest above the middle; roots thick or slender, 2–8 mm diam.
41a. Cataphylls promptly weathering to fibers; petioles either sharply trapezoidal and more than 1.5 cm diam. or subquadrangular with 3 sharp adaxial ribs and less than 9 mm diam.
42a. Plants terrestrial; petioles subquadrangular, less than 9 mm diam.; blades moderately thin, long-attenuate at base; primary lateral veins 8–12 pairs; spathe thin, green, linear-lanceolate, spreading-reflexed to spreading (remaining flat, never strongly reflexed); spadix less than 8 mm diam.; Costa Rica and Panama; 0–900 m ..... *A. acutifolium* Engl.
42b. Plants epiphytic or sometimes on rocks; petioles usually trapezoidal, mostly more than 10 mm diam.; blades moderately coriaceous, acute to obtuse at base; primary lateral veins usually more than 12 pairs; spathe coriaceous, often heavily tinged purple, usually narrowly triangular, usually strongly reflexed (the margins rolled under in age); spadix usually more than 1.5 cm diam.; Atlantic slope, Mexico to Honduras; sea level to usually less than 1,000 m ..... *A. schlechtendalii* Kunth subsp. *schlechtendalii*
41b. Cataphylls persisting mostly intact; petioles bluntly quadrangular to subquadrangular, sometimes bluntly 3-ribbed adaxially.
43a. Petioles prominently 3-ribbed abaxially; cataphylls persisting intact, conspicuous, only rarely weathered; Nicaragua to Costa Rica; sea level to 600 m ..... *A. upalaense* Croat & R. A. Baker
43b. Petioles not prominently ribbed abaxially; cataphylls thin, often weathered to reticulate fibers in part.
44a. Spadix bluntly tapered, more than 17 mm diam. at base; roots ascending to descending, greenish to tan, 3–8 mm diam.; fruits bright red; Mexico to Nicaragua; 0–1,600 m ..... *A. schlechtendalii* Kunth
44b. Spadix long-tapered, less than 10 mm diam. at base; roots mostly directed upward, whitish, ca. 1 mm diam.; fruits cream to greenish yellow or pale orange; Costa Rica to Panama; 0–1,200 m ..... *A. fatoense* K. Krause

36b. Petioles ± D-shaped to subterete in cross section (sometimes bluntly 4-sided in *A. pseudospectabile*).
45a. Plants pendent; primary lateral veins more than 30 pairs; premontane wet or premontane rainforest life zones, western Panama; 1,250–1,500 m ..... *A pseudospectabile* Croat
45b. Plants with leaves erect, rosulate; primary lateral veins less than 15 pairs.
46a. Peduncle mostly shorter than petioles, rarely more than twice as long as spadix; spadix cylindroid; tropical dry forest or drier parts of tropical moist forest life zones ..... *A. cubense* Engl.
46b. Peduncles usually much longer than petioles, always more than twice as long as the spadix; spadix long-tapered toward apex.
47a. Blades elliptic to narrowly elliptic, broadest at about the middle, less than 3× longer than wide.
48a. Blades usually more than 15 cm wide, drying brown to greenish brown and moderately coriaceous; spathe more than 2.5 cm wide; spadix green becoming reddish brown; Mexico (Guerrero and Oaxaca); to 850 m ..... *A. nizandense* Matuda
48b. Blades less than 15 cm wide, drying pale yellow-green, thin; spathe 1 cm wide or less; spadix yellow; Costa Rica; 300–400 m ..... *A. acutifolium* Engl. var. *herrerae* Croat
47b. Blades oblanceolate to obovate, broadest above the middle, more than 3.5× longer than wide.
49a. Inflorescence erect; spathe ovate to broadly ovate, less than 3× longer than wide; cataphylls lanceolate; fruits pale yellow or unknown; western Mexico.

50a. Spathe erect, usually dark purple on inside, less than 6 cm long; spadix clavate, broadest near the apex; fruits unknown; endemic to Michoacán; near sea level ..... *A. sarukhanianum* Croat & Haager

50b. Spathe spreading, green, at most tinged with purple on inside, more than 13 cm long; spadix tapered toward apex, broadest at or near the base; fruits yellow, greenish at tip; Nayarit, Jalisco and Michoacán; 450–1,000 m ..... *A. halmoorei* Croat

49b. Inflorescence usually pendent; spathe lanceolate-linear, more than 5× longer than wide; cataphylls cucullate, fist-shaped; fruits red; Mexico to Colombia; 0–1,400 m ..... *A. salviniae* Hemsley

1b. Species of South America.

51a. Collective vein arising from the base or at least below the middle of the leaf blade.

52a. Spadix greenish or whitish at anthesis.

53a. Spadix bluish green and appearing glaucous at anthesis.

54a. Spadix 14–33 cm long; leaf blades drying coriaceous; central Colombia; 500–2,100 m ..... *A. glaucospadix* Croat

54b. Spadix 4–8.5 cm long; leaf blades drying thin; widespread in western Amazonia; 100–870 m ..... *A. oxycarpum* Poeppig

53b. Spadix not bluish green or glaucous at anthesis.

55a. Primary lateral veins prominently and sharply raised on upper surface (even when fresh); eastern slopes of Andes in Ecuador and northern Peru; 1,000–2,500 m ..... *A. penningtonii* Croat

55b. Primary lateral veins not prominently and sharply raised on upper surface.

56a. Primary lateral veins toward base of leaf blade perpendicular to midrib to retrorse to 130° angle; central Peru; 500–1,800 m ..... *A. latissimum* Engl.

56b. Primary lateral veins all ascending.

57a. Petioles mostly 2–10-ribbed abaxially.

58a. Spadix stipitate 5.5–7 cm; leaf blades drying thin; western slopes of Andes in Ecuador; 510–690 m ..... *A. bucayanum* Croat

58b. Spadix sessile or subsessile; leaf blades drying subcoriaceous to coriaceous.

59a. Primary lateral veins fewer than 15 per side; cataphylls hooked; central Colombia; 900–1,750 m ..... *A. caucavallense* Croat

59b. Primary lateral veins more than 15 per side; cataphylls straight; western slopes of Andes in Ecuador.

60a. Leaf blades less than 20 cm wide; peduncle less than 40 cm long; spadix less than 10 cm long; western Loja; 1,400–2,700 m ..... *A. lennartii* Croat

60b. Leaf blades more than 20 cm wide; peduncle more than 40 cm long; spadix more than 10 cm long; Bolívar and Chimborazo; 1,200–2,150 m ..... *A. campii* Croat

57b. Petioles mostly rounded or only 1-angled abaxially.

61a. Spadix deflexed to reflexed, held at 130–160° angle from peduncle; western slopes of Andes in Ecuador; 300–400 m ..... *A. oxyphyllum* Sodiro

61b. Spadix not deflexed or reflexed, held ± 180° from peduncle.

62a. Species of the Amazon basin and drainage system.

63a. Leaf blades broadly elliptic to broadly elliptic with flat margins; Peru (San Martín) or Venezuela (Amazonas).

64a. Blades epunctate on lower surface; collective veins arising from the base of the blade; San Martín, Peru; 400–500 m ..... *A. knappiae* Croat

64b. Blades conspicuously glandular-punctate on the lower surface; collective veins lacking or arising from the uppermost primary lateral veins. 420 m ..... *A. vinillense* Bunting

63b. Leaf mostly oblanceolate, with conspicuously undulate margins.

65a. Primary lateral veins fewer than 10 per side; San Martín, Peru; 130–750 m ..... *A. llewelynii* Croat

65b. Primary lateral veins more than 10 per side; Ecuador to southern Peru; 950–2,750 m ..... *A. dombeyanum* Brongn. ex Schott

62b. Species occurring on western slopes of Andes in Ecuador.
66a. Peduncle more than 3× longer than petioles; El Oro and Cotopaxi; 2,100–2,500 m ..... *A. angustilaminatum* Engl. subsp. *cibuserpentis* Croat
66b. Peduncle less than 3× longer than petioles.
67a. Petioles sharply triangular-winged; blades markedly long-attenuate in lower half; terrestrial; 80–400 m ..... *A. palenquense* Croat
67b. Petioles subterete to D-shaped; blades acute or at most abruptly attenuate at base, not markedly long-attenuate in lower half of blade; usually epiphytic.
68a. Blades mostly more than 15 cm wide, less than 7× longer than wide; central and northern Ecuador; 250–1,500 m ..... *A. holmnielsenii* Croat
68b. Blades less than 15 cm wide, more than 7× longer than wide.
69a. Blades usually pendent, matte and velvety on the upper surface; petioles terete to subterete; Los Ríos and Pichincha; 650–1,200 m ..... *A. acutissimum* Engl.
69b. Blades stiffly erect-spreading, usually semiglossy on upper surface; petioles sharply D-shaped; widespread in western Ecuador; 50–1,330 (2,000) m ..... *A. obscurinervium* Croat

52b. Spadix reddish or purplish at anthesis.
70a. Species of the Amazon basin and drainage system.
71a. Spadix longer than peduncle; La Paz, Bolivia; 1,000–1,400 m ..... *A. solomonii* Croat
71b. Spadix shorter than peduncle.
72a. Leaf blades with primary lateral veins mostly more than 15 per side; occurring mostly above 800 m (origin of *A. martianum* unknown).
73a. Leaf blades less than 10 cm wide.
74a. Blades less than 2.5× longer than the petioles; cataphylls persisting intact to semi-intact; Peru and Bolivia; 890–1,700 m ..... *A. ottonis* K. Krause
74b. Blades more than 2.5× longer than the petioles; cataphylls persisting at a reticulum of pale fibers.
75a. Petioles subtriangular; spadix with 5–7 flowers visible per spiral; dried pistils protruding well above the tepals, blackened with pale raphide cells visible; southern Ecuador to Bolivia; 2,200–2,400 m ..... *A. soukupii* Croat
75b. Petioles D-shaped; spadix with 8–11 flowers visible per spiral; dried pistils rounded at apex and not emerging above tepals, yellow-brown and lacking raphide cells; eastern slopes of the Andes in Ecuador (Tunguragua, Pastaza and Morona Santiago); 970–1,600 m ..... *A. fasciale* Sodiro
73b. Leaf blades more than 10 cm wide.
76a. Leaf blades more than 20 cm wide.
77a. Primary lateral veins more than 25 per side; petioles triangular, acutely angled abaxially; eastern slopes of Andes in Ecuador; 600–1,830 m ..... *A. santiagoense* Croat
77b. Primary lateral veins fewer than 25 per side; petioles mostly D-shaped, rounded abaxially.
78a. Leaf blades about as long as or scarcely longer than the petioles; blades broadest at or below the middle; peduncle less than 2× longer than petiole; origin unknown, said to be from the Guianas ..... *A. martianum* K. Koch & Kolb
78b. Leaf blades much longer than the petioles; blades broadest above the middle (rarely near the middle); peduncle more than 2× longer than petiole; Ecuador to southern Peru; (370)950–2,760 m ..... *A. dombeyanum* Brongn. ex Schott
76b. Leaf blades mostly less than 20 cm wide.
79a. Leaf blades conspicuously quilted (i.e., with the leaf tissue conspicuously raised between the primary lateral veins), with primary lateral veins ascending and then spreading retrorsely at 30–70° angle; Huánuco, Peru; 650–800 m ..... *A. reflexinervium* Croat
79b. Leaf blades not quilted, with primary lateral veins all ascending.

80a. Primary veins prominently and sharply raised on upper surface (even on drying); eastern slopes of Andes in Ecuador and northern Peru; (800)1,000–2,500 m ..... *A. penningtonii* Croat

80b. Primary lateral veins not prominently and sharply raised on upper surface.

81a. Leaf blades oblong; peduncle less than 3× longer than petiole; eastern slopes of Andes in Ecuador; 970–1,600 m ..... *A. fasciale* Sodiro

81b. Leaf blades mostly oblanceolate; peduncle more than 3× longer than petiole; Ecuador to southern Peru; 950–2,760 m ..... *A. dombeyanum* Brongn. ex Schott

72b. Leaf blades with primary lateral veins 15 or fewer per side; occurring mostly below 800 m.

82a. Leaf blades with primary lateral veins toward base perpendicular to midrib to retrorse; central Peru; 500–1,800 m ..... *A. latissimum* Engl.

82b. Leaf blades with primary lateral veins all ascending.

83a. Leaf blades over 4× longer than broad or ≤2× longer than broad.

84a. Leaves spreading-pendent; blades oblong to oblanceolate, over 4× longer than broad; Ecuador and adjacent Peru and Colombia; 90–550 m ..... *A. pendulifolium* N. E. Br.

84b. Leaves erect or spreading; blades elliptic to broadly ovate-elliptic or broadly lanceolate, ≤2× longer than broad.

85a. Blades obtuse to rounded or cuneate at base; basal veins usually 1 pair, rarely 2 pairs, merging with the margin in the lower ¼ of the blade; Emma mountains, Surinam; 850 m ..... *A. lanjouwii* Jonker & Jonker

85b. Blades shallowly cordate at base; basal veins 3–4 pairs, at least the uppermost joining the margin well near or above the middle of the blade; Cerro Neblina and Cerro Yapacana, Amazonas, Venezuela; 780–825 m ..... *A. wurdackii* Bunting

83b. Leaf blades mostly between 4 and 2× longer than broad.

86a. Peduncle less than 10 cm long; spadix less than 5 cm long; leaf blades quilted and velvety; known only from Río Sucusari, Loreto, Peru; below 200 m ..... *A. willifordii* Croat

86b. Peduncle more than 10 cm long at anthesis; spadix more than 5 cm long; leaf blades not quilted or velvety.

87a. Geniculum appearing remote from base of blade by 4–11 cm; Amazonas, Brazil ..... *A. krukovii* Croat

87b. Geniculum at base of blade, not appearing remote.

88a. Leaf blades mostly more than 40 cm long; western Amazonia; mostly below 500 m.

89a. Blades usually narrowly to broadly oblanceolate, long-attenuate or rarely acute at base ..... *A. atropurpureum* R. Schultes & Maguire var. *arenicola* Croat

89b. Blades ovate-elliptic, rounded at base (sometimes acutely decurrent onto petiole) ..... *A. atropurpureum* R. Schultes & Maguire var. *thomasii* Croat

88b. Leaf blades less than 40 cm long.

90a. Leaf blades broadest near middle, drying pale green; tertiary veins etched on upper surface when fresh; northwestern Amazonia; below 160 m.

91a. Blades drying pale gray-green, less than 14 cm wide, usually less than 12 cm wide, narrowly acute or at least prominently decurrent at base; the spathe inserted at ca. 90° angle on peduncle; western margin of Amazon basin in Acre, Brazil, and Loreto, Peru; 120–160 m ..... *A. atropurpureum* R. Schultes & Maguire var. *atropurpureum*

91b. Blades drying dark yellow-green to yellow-brown, more than 12 cm, (usually more than 14 cm) wide, usually obtuse to rounded at base, never narrowly acute or decurrent at base; spathe inserted at ca. 45° angle on peduncle; Surinam; 850 m ..... *A. lanjouwii* Jonker & Jonker

90b. Leaf blades broadest below middle, drying dark, mostly brown; tertiary veins not etched on upper surface; known only from near Tarapoto, San Martín, Peru ..... *A. basirotundum* Croat

70b. Species of northern and central and Pacific coastal Colombia, western slopes of Andes in Ecuador and northern coastal Peru or eastern coastal Brazil, not occurring in the Amazon basin or drainage system.
92a. Leaf blades usually less than 15 cm wide.
93a. Primary lateral veins near middle of leaf blade more than 2 cm apart.
94a. Terrestrial; leaf blades oblong-linear, less than 7 cm wide; coastal Ecuador ..... *A. linquifolium* Engl.
94b. Epiphytic; leaf blades oblong-oblanceolate, more than 7 cm wide; Tumbes, Peru; 600–800 m ..... *A. simpsonii* Croat
93b. Primary lateral veins at middle of leaf blade mostly less than 2 cm apart.
95a. Primary lateral veins sharply raised on upper surface (even when fresh); western slopes of Andes in Ecuador; 2,000–3,000 m ..... *A. pallatangense* Engl.
95b. Primary lateral veins not sharply raised on upper surface.
96a. Leaf blades with margins conspicuously concave toward base; western slopes of Andes in Ecuador; 150–300 m ..... *A. palenquense* Croat
96b. Leaf blades with margins straight or convex toward base.
97a. Petioles sharply triangular, mostly more than 16 cm long; western slopes of Andes in Ecuador; 200–1,300 m ..... *A. napaeum* Engl.
97b. Petioles D-shaped, subterete or obscurely triangular, mostly less than 16 cm long.
98a. Leaf blades truncate to narrowly rounded at base; Ecuador; 2,135–2,500 m ..... *A. angustilaminatum* Engl. subsp. *cibuserpentis* Croat
98b. Leaf blades acute to attenuate at base.
99a. Leaf blades mostly more than 50 cm long, 4.5–6.6× longer than petioles; spadix dark purple; Pichincha, Ecuador; ca. 1,200 m ..... *A. angustilaminatum* Engl. subsp. *angustilaminatum*
99b. Leaf blades mostly less than 50 cm long; 2.5–4.5× longer than petioles; spadix maroon to brownish (orange-brown, brown to brownish purple); Carchí, Ecuador, Nariño, Colombia; 1,200–2,600 m ... *A. carchiense* Croat
92b. Leaf blades usually more than 15 cm wide.
100a. Petioles triangular or terete.
101a. Petioles terete; spathe 2.5–4.3 cm wide, erect; fruits dirty white to pale violet; southeastern coastal Brazil; 0–250 m ..... *A. coriaceum* G. Don in Sweet
101b. Petioles triangular; spathe 0.4–2.5 cm wide, reflexed to spreading; fruits dirty white; western slopes of Andes in Ecuador and Colombia.
102a. Leaf blades with margins conspicuously concave toward base; 80–400 m ..... *A. palenquense* Croat
102b. Leaf blades with margins straight or convex toward base; 200–1,300 m ..... *A. napaeum* Engl.
100b. Petioles usually D-shaped.
103a. Primary lateral veins fewer than 20 per side.
104a. Fruits orange; roots glabrous and minutely but conspicuously warty; cataphylls straight; Magdalena, Colombia, near Minca ..... *A. johnsoniae* Croat
104b. Fruits violet-purple; roots pubescent, not warty; cataphylls hooked; central Colombia; 900–1,750 m ..... *A. caucavallense* Croat
103b. Primary lateral veins 20 or more per side.
105a. Leaf blades rounded to truncate at base, about as long as petiole or rarely twice as long; origin unknown ..... *A. martianum* K. Koch & Kolb
105b. Leaf blades acute to attenuate at base, 2–8× longer than petiole.
106a. Spadix purplish brown, stipitate 2.5–3 cm; Manabí, Ecuador; 450 m ..... *A. manabianum* Croat
106b. Spadix dark purple to reddish violet, subsessile.
107a. Spadix more than 30× longer than thick; leaf blades long-attenuate at base; Nariño, Colombia; 900–1,000 m ..... *A. narinoense* Croat

107b. Spadix less than 30× longer than thick; leaf blades acute to obtuse or cuneate at base; Ecuador; 210–250 m ..... *A. sparreorum* Croat

51b. Collective vein arising from above or near middle of leaf blade or absent.
108a. Spadix red, reddish, maroon, or purplish to violet-purple.
109a. Peduncle less than 5× longer than petiole.
110a. Species of Amazon basin and drainage system (Brazilian highlands, Bolivia, Paraguay, Argentina).
111a. Leaf blades ≤3× longer than broad.
112a. Petioles mostly subterete in cross section.
113a. Leaf blades subcordate at base, thickly coriaceous; peduncle more than 50 cm long.
114a. Leaf blade stipitate, the midrib naked beyond the base of the blade for a distance of up to 5 cm before reaching the geniculum (the geniculum appearing remote), or the blade at least decurrent and the lowermost primary lateral veins naked at base for 1.5–2 cm; Venezuela, Amazonas; 10–150 m ..... *A. guanchezii* Bunting
114b. Leaf blade not stipitate at base, the geniculum not appearing remote from the base of the blade.
115a. Blade ovate, 1.5–1.7× longer than wide, dark glandular-punctate on lower surface; spathe decurrent for less than 1 cm; Venezuela, Amazonas; 1,350 m ..... *A. iramirezae* Bunting
115b. Blades ovate-elliptic, 1.9–2.2× longer than wide, epunctate; spathe decurrent for 2–7.5 cm; Venezuela, Amazonas; 725–825 m ..... *A. wurdackii* Bunting
113b. Leaf blades attenuate to obtuse at base, chartaceous to moderately coriaceous; peduncle less than 50 cm long.
116a. Blades obtuse to rounded or sometimes cuneate at base, never attenuate; Surinam; 850 m ..... *A. lanjouwii* Jonker & Jonker
116b. Blades attenuate at base; upper Amazon basin; less than 300 m.
117a. Petioles less than 25 cm long; geniculum at base of leaf blade; Loreto, Peru; 100–160 m ..... *A. uleanum* Engl. var. *nanayense* Croat
117b. Petioles more than 25 cm long; geniculum appearing remote from base of leaf blade by 4–20 cm; Acre State, Brazil ..... *A. pranceanum* Croat
112b. Petioles variously shaped in cross section but never subterete.
118a. Spadix longer than peduncle; infructescence with apical ca. ⅓ withered; cataphyll fibers fine, hairlike, reddish brown; Peru to Bolivia, Paraguay, and Brazil; 50–900 m ..... *A. plowmanii* Croat
118b. Spadix shorter than peduncle; infructescence usually not withered in apical ⅓; cataphyll fibers various, usually not fine and hairlike.
119a. Leaf blade broadest at or below middle, up to 41 cm long; spadix less than 15× longer than thick; known only from vicinity of Tarapoto, San Martín, Peru ..... *A. basirotundum* Croat
119b. Leaf blade broadest above the middle, or if broadest near or below middle, then spadix more than 15× longer than thick; leaf blades mostly longer.
120a. Spadix more than 40× longer than thick, 3–4 mm diam. midway (when dried); known only from Colombia (Vaupés, Amazonas) ..... *A. vaupesianum* Croat
120b. Spadix less than 40× longer than thick, or if more than 40× longer than thick, then more than 5 mm diam.
121a. Primary lateral veins toward base of leaf blade perpendicular to retrorse to 130° to midrib; central Peru; 500–1,800 m ..... *A. latissimum* Engl.
121b. Primary lateral veins all ascending, never retrorse.
122a. Cataphylls hooked or cucullate.
123a. Inflorescence erect-spreading; leaf blades usually matte on upper surface (when

fresh); above 400 m (up to 1,800 m) on eastern slopes of Andes in Colombia and Ecuador ..... *A. harlingianum* Croat

123b. Inflorescence pendent to spreading-pendent; leaf blades semiglossy on upper surface (when fresh); western and northern Amazonia; below 300 m.

124a. Peduncle 5–6× longer than petiole, strictly pendent, 3–5 mm diam. at anthesis; Venezuela in Amazonas and Bolívar, northern Pará State in Brazil ..... *A. cataniapoense* Croat

124b. Peduncle 4–12× longer than petiole, spreading to spreading-pendent, 6–11 mm diam. at anthesis; Upper Amazon basin, western Brazil (Amazonas) Peru, Colombia, and Ecuador ..... *A. loretense* Croat

122b. Cataphylls straight, lanceolate.

125a. Leaf blades frequently with glandular punctations and/or pustules (at least abaxially); habit mostly terrestrial or epilithic; widespread in Brazil and Colombia, Venezuela, and the Guianas.

126a. Spathe usually withered at anthesis.

127a. Spathe thin, caducous, 5.5–11.5 cm long; western to northeastern Colombia, western Venezuela, Panama; sea level to 1,000 (2,430) m ..... *A. fendleri* Schott

127b. Spathe subcoriaceous, not caducous, 11–50 cm long; Trinidad and Tobago, Venezuela, Guianas, Amapá in Brazil; mostly below 500 m ..... *A. jenmanii* Engl.

126b. Spathe not withered at anthesis.

128a. Stems erect; northern Amazon basin, rarely south of the Río Amazonas (middle Río Tocantins).

129a. Leaf blades rounded to subtruncate at base, mostly drying greenish; stipe 15–40 mm long; southeastern Colombia, Amazonas, and Bolívar in Venezuela; 75–380 m ..... *A. bonplandii* Bunting subsp. *cuatrecasii* Croat

129b. Leaf blades attenuate to acute or obtuse at base, usually drying brown or yellowish; stipe lacking or to 20 mm long.

130a. Leaf blades usually elliptic to broadly elliptic; usually 3–6× longer than petiole; petiole rarely exceeding 30 cm long; southeastern Colombia, southern Venezuela, northwestern Brazil; mostly below 500 m ..... *A. bonplandii* Bunting subsp. *bonplandii*

130b. Leaf blades usually oblanceolate to obovate; usually about twice as long as the petiole; Surinam, southern Venezuela; 400–1,400 m ..... *A. bonplandii* Bunting subsp. *guayanum* (Bunting) Croat

128b. Stem creeping horizontally; Mato Grosso, Goiás, southern Pará and Rondônia in Brazil ..... *A. lindmanianum* Engl.

125b. Leaf blades without glandular punctations or pustules; habit mostly epiphytic; mostly occurring in Peru and Ecuador.

131a. Cataphylls persisting as a skeleton of fine, pale fibers; leaf blades mostly drying green, with primary lateral veins conspicuously orangish.
132a. Inflorescence spreading-pendent; peduncle 23–54 cm long; known only from Pastaza, Ecuador; 300 m ..... *A. ernestii* Engl. var. *oellgaardii* Croat
132b. Inflorescence erect; peduncle usually 3–25 cm long; widespread in western Amazonia; below 500 m ..... *A. ernestii* Engl. var. *ernestii*
131b. Cataphylls persisting semi-intact and brown, with the fibers relatively inconspicuous; leaf blades mostly drying brown, with primary lateral veins brownish or yellowish.
133a. Primary lateral veins 10–23 per side.
134a. Epiphytic; petioles rounded and unribbed or 3–5-ribbed abaxially; peduncle 21–50 cm long; spadix salmon-pink to pale violet-purple; eastern slopes of Andes in Colombia and Ecuador; 440–1,800 m ..... *A. harlingianum* Croat
134b. Terrestrial; petioles 5–8-ribbed abaxially; peduncle 50–91 cm long; spadix dark purple; Imbabura, Ecuador; 900–1,500 m ..... *A. leonianum* Sodiro
133b. Primary lateral veins mostly 5–10 per side.
135a. Geniculum appearing remote from base of blade by up to 16 cm; petioles narrowly and obtusely sulcate adaxially with blunt margins; San Martín and Amazonas, Peru; 530–1,160 m ..... *A. remotigeniculatum* Croat
135b. Geniculum not appearing remote; petioles convex to broadly sulcate adaxially with sharp margins.
136a. Spadix appearing glaucous, mostly 18–50× longer than broad; Loreto, Peru, and adjacent Colombia, Ecuador, and Brazil; below 550 m ..... *A. uleanum* Engl. var. *uleanum*
136b. Spadix not appearing glaucous, 6–18× longer than broad; San Martín, Peru; 360–700 m ..... *A. tarapotense* Engl.

111b. Leaf blades usually more than 3× longer than broad.
137a. Primary lateral veins retrorse toward base of leaf blade or throughout its length.
138a. Leaf blades to 18 cm wide, obtuse to shallowly cordate at base, conspicuously quilted, with conspicuously retrorse, arcuate primary lateral veins throughout their length; known only from vicinity of Tingo María (Huánuco), Peru; 650–800 m ..... *A. reflexinervium* Croat
138b. Leaf blades to 36.5 cm wide, acute to attenuate at base, weakly bullate at most, with conspicuously retrorse primary lateral veins only toward base of leaf blade; central Peru; 500–1,800 m ..... *A. latissimum* Engl.
137b. Primary lateral veins all ascending.
139a. Peduncle more than 3× longer than petiole.
140a. Spadix pale and appearing glaucous.
141a. More than 6 flowers visible in either spiral; western Amazonia; below 550 m ..... *A. uleanum* Engl. var. *uleanum*

141b. Fewer than 6 flowers visible in either spiral; Loreto, Peru, 100–160 m ..... *A. uleanum* Engl. var. *nanayense* Croat

140b. Spadix usually not pale, not appearing glaucous.
142a. Spathe usually withered at anthesis.
143a. Tertiary veins prominently etched on upper surface when fresh; western Amazonia; 100–560 m ..... *A. atropurpureum* R. Schultes & Maguire var. *arenicola* Croat
143b. Tertiary veins not prominently etched on upper surface when fresh.
144a. Spathe thin, caducous, 5.5–11 cm long; western-central to northeastern Colombia, western Venezuela, Panama; sea level to 1,000(2,430) m ..... *A. fendleri* Schott
144b. Spathe subcoriaceous, not caducous, 11–50 cm long; Trinidad and Tobago, Guianas, Amapá in Brazil; mostly below 500 m ..... *A. jenmanii* Engl.
142b. Spathe not withered at anthesis.
145a. Cataphylls hook-shaped or cucullate.
146b. Inflorescence erect-spreading; leaf blades usually matte on upper surface (when fresh); lower eastern slopes of Andes in Colombia and Ecuador; 440–1,800 m ..... *A. harlingianum* Croat
146b. Inflorescence pendent; leaf blades semiglossy on upper surface (when fresh); in Amazonas and Bolívar, Venezuela, Pará in Brazil; below 300 m ..... *A. cataniapoense* Croat
145b. Cataphylls straight, lanceolate.
147a. Leaf blade with tertiary veins conspicuously etched on upper surface when fresh; central Peru; (240)320–770 m ..... *A. pachylaminum* Croat
147b. Leaf blade with tertiary veins not conspicuously etched, mostly obscure, when fresh.
148a. Petioles rounded abaxially.
149a. Primary lateral veins 10–21 per side.
150a. Petioles ca. 8 cm long; leaf blades ca. 5.4× longer than broad; known only from the Serranía de Cutucú in Morona-Santiago, Ecuador; 1,300 m ..... *A. bushii* Croat
150b. Petioles 10–30 cm long; leaf blades usually less than 5× longer than broad; central Ecuador to southern Peru; 950–2,760 m ..... *A. dombeyanum* Brongn. ex Schott
149b. Primary lateral veins 5–10 per side.
151a. Leaf blades rounded to subtruncate at base, mostly drying greenish; stipe 15–40 mm long; southeastern Colombia, Amazonas and Bolívar in Venezuela; 75–380 m ..... *A. bonplandii* Bunting subsp. *cuatrecasii* Croat
151b. Leaf blades acute to attenuate at base, mostly drying brown to yellowish; stipe 3–20 mm long; southeastern Colombia, southern Venezuela, northern Brazil; mostly below 500 m ..... *A. bonplandii* Bunting subsp. *bonplandii*
148b. Petioles (1)3–5(8)-ribbed abaxially.
152a. Primary lateral veins 10–16 per side.
153a. Peduncle less than 50 cm long; spadix 7–8 cm long; epiphytic; known only from Pastaza, Ecuador; 300 m ..... *A. ernestii* Engl. var. *oellgaardii* Croat

153b. Peduncle more than 50 cm long; spadix over 20 cm long; terrestrial; known only from Imbabura, Ecuador; 900–1,500 m ..... *A. leonianum* Sodiro

152b. Primary lateral veins 4–10 per side.

154a. Leaf blades subcoriaceous, oblanceolate to oblong-oblanceolate, without glandular punctations; southern Brazil, Bolivia, Paraguay, northern Argentina; 150–1,700 m ..... *A. paraguayense* Engl. var. *paraguayense*

154b. Leaf blades mostly coriaceous, mostly elliptic to broadly elliptic, usually with glandular punctations below; southeastern Colombia, southern Venezuela, northern Brazil; mostly below 500 m ..... *A. bonplandii* Bunting subsp. *bonplandii*

139b. Peduncle ≤3× longer than petiole.

155a. Spadix pale and appearing glaucous.

156a. Peduncle 2.5–9 cm long; spadix 1.7–4.7 cm long; leaves quilted and velvety; known only from Río Sucusari, Loreto, Peru ..... *A. willifordii* Croat

156b. Peduncle 14–38 cm long; spadix 5–15 cm long; leaves not quilted or velvety.

157a. More than 6 flowers visible in either spiral; western Amazonia; below 550 m ..... *A. uleanum* Engl. var. *uleanum*

157b. Fewer than 6 flowers visible in either spiral; Loreto, Peru; 100–160 m ..... *A. uleanum* Engl. var. *nanayense* Croat

155b. Spadix usually not pale, not appearing glaucous.

158a. Spathe very thin, usually withered at anthesis.

159a. Tertiary veins prominently etched on upper surface when fresh; western Amazonia; below 560 m ..... *A. atropurpureum* R. Schultes & Maguire var. *arenicola* Croat

159b. Tertiary veins not prominently etched on upper surface when fresh; western to northeastern Colombia, western Venezuela, Panama; sea level to 1,000(2,430) m ..... *A. fendleri* Schott

158b. Spathe moderately thick, not withered at anthesis.

160a. Spadix longer than peduncle; infructescence with apical ca. ⅓ withered; cataphyll fibers fine, hairlike, reddish brown; Peru to Bolivia, Paraguay and Brazil; 50–900 m ..... *A. plowmanii* Croat

160b. Spadix shorter than peduncle, usually much shorter; infructescence usually not withered in apical ⅓; cataphyll fibers various, usually not fine and hairlike.

161a. Leaf blade with tertiary veins conspicuously etched on upper surface when fresh; central Peru; (240)320–770 m ..... *A. pachylaminum* Croat

161b. Leaf blade with tertiary veins not conspicuously etched above, mostly obscure when fresh.

162a. Leaves and inflorescence pendent to spreading-pendent; petioles usually more than 30 cm long; spadix more than 20 cm long; Ecuador and adjacent Peru and Colombia; 90–550 m ..... *A. pendulifolium* N. E. Br.

162b. Leaves and inflorescence erect to erect-spreading; petioles mostly less than 30 cm long; spadix mostly less than 20 cm long.

163a. Leaf blades usually with conspicuous glandular punctations (at least abaxially).

164a. Leaf blades rounded to subtruncate at base, mostly drying greenish; stipe 15–40 mm long; southeastern Colombia, Amazonas and Bolívar

in Venezuela; 75–380 m ..... *A. bonplandii* Bunting subsp. *cuatrecasii* Croat

164b. Leaf blades acute to attenuate at base, mostly drying brown or yellowish; stipe 3–20 mm long; southeastern Colombia, southern Venezuela, northern Brazil; mostly below 500 m ..... *A. bonplandii* Bunting subsp. *bonplandii*

163b. Leaf blades without glandular punctations.

165a. Cataphylls persisting as an intact network of fine, pale fibers; primary lateral veins usually drying conspicuously orange on lower surface.

166a. Inflorescence spreading-pendent; peduncle more than 20 cm long; known only from Pastaza, Ecuador ..... *A. ernestii* Engl. var. *oellgaardii* Croat

166b. Inflorescence erect; peduncle usually less than 20 cm long; widespread in western Amazonia; below 500 m ..... *A. ernestii* Engl. var. *ernestii*

165b. Cataphylls persisting semi-intact and brown with usually inconspicuous, mostly coarse fibers; primary lateral veins not drying orange.

167a. Petioles 1–3-ribbed abaxially; southern Brazil, Bolivia, Paraguay, northern Argentina; 150–1,700 m ..... *A. paraguayense* Engl. var. *paraguayense*

167b. Petioles rounded abaxially; Brazil, Ecuador, and Peru.

168a. Primary lateral veins 10–20 per side; peduncle 3–7× longer than petiole; central Ecuador to southern Peru; 950–2,760 m ..... *A. dombeyanum* Brongn. ex Schott

168b. Primary lateral veins 6–10 per side; peduncle less than 3× longer than petiole.

169a. Stem erect; petioles medially 1-ribbed adaxially; epiphytic; known only from Napo, Ecuador; 600 m ..... *A. tenaense* Croat

169b. Stem usually horizontal and creeping; petioles flat to slightly sulcate adaxially; terrestrial or epilithic, rarely epiphytic; Brazil in Mato Grosso, Goiás, Pará, Rondônia ..... *A. lindmanianum* Engl.

110b. Species of western slopes of Andes, northern Colombia and Venezuela, southeastern coastal Brazil; not occurring in the Amazon basin.

170a. Cataphylls cucullate or hook-shaped.

171a. Cataphylls cucullate.

172a. Blades usually more than 4× longer than wide, the margins usually sinuate and markedly undulate; petioles usually 1–4-ribbed abaxially; inflorescence usually erect-spreading; spadix reddish to purplish violet, not glaucous; coastal Ecuador and Peru; mostly dry regions, sea level to 890 m ..... *A. barclayanum* Engl.

172b. Blades usually less than 4× longer than wide, the margins not at all sinuate and only weakly undulate; petioles rounded abaxially; inflorescence usually pendent; spadix pale lavender, glaucous; northern Colombia to Nicaragua; humid to wet regions, sea level to 1,600 m ..... *A. salviniae* Hemsley

171b. Cataphylls hook-shaped.
173a. Primary lateral veins departing midrib at 70–90° angle; peduncle 1–2× longer than petiole; central Colombia; 900–1,750 m ..... *A. caucavallense* Croat
173b. Primary lateral veins departing midrib at 40–50° angle; peduncle 3–6× longer than petiole; coastal Ecuador; sea level to 400 m ..... *A. asplundii* Croat

170b. Cataphylls straight.
174a. Spathe usually withered at anthesis (at least on dried specimens).
175a. Spathe thin, caducous, 5.5–11 cm long; Panama, western to northeastern Colombia, western Venezuela; sea level to 1,000(2,430) m ..... *A. fendleri* Schott
175b. Spathe subcoriaceous, not caducous, 11–50 cm long; Trinidad and Tobago, Guianas, Amapá in Brazil mostly below 500 m ..... *A. jenmanii* Engl.
174b. Spathe not withered at anthesis.
176a. Primary lateral veins 16–30 per side; leaf blades drying distinctly green; western slopes of Andes in Ecuador.
177a. Petioles broadly triangular; 4–6 flowers visible per spiral; 200–1,300 m ..... *A. napaeum* Engl.
177b. Petioles D- or U-shaped; usually more than 6 flowers visible per spiral.
178a. Petioles 15–38 cm long; leaf blades 46–90 cm long, 10–20 cm wide; Los Ríos and Cotopaxi, Ecuador; 210–250 m ..... *A. sparreorum* Croat
178b. Petioles 7–15 cm long; leaf blades 90–125 cm long, 20–34 cm wide; Esmeraldas, Los Ríos and Pichincha, Ecuador; sea level to 400 m ..... *A. asplundii* Croat
176b. Primary lateral veins 5–17 per side; leaf blades mostly drying brown; northern South America to Central America, Cuba, coastal Brazil.
179a. Petioles C-shaped, narrowly and deeply sulcate with usually blunt margins adaxially, rounded abaxially; Brazil in Minas Gerais, Rio de Janeiro and Espírito Santo ..... *A. solitarium* (Vell. Conc.) Schott
179b. Petioles not C-shaped, usually D-shaped, mostly flattened or shallowly sulcate with sharp margins adaxially, generally flat or 1–several-ribbed abaxially.
180a. Spadix more than 15× longer than thick; northern Venezuela, northwestern Colombia, Curaçao; sea level to 1,800 m ..... *A. crassinervium* (Jacq.) Schott
180b. Spadix less than 15× longer than thick.
181a. Peduncle less than 30 cm long; petioles mostly rounded abaxially; more than 10 flowers visible in either spiral; northern Colombia and Venezuela, Cuba, to Central America ..... *A. cubense* Engl.
181b. Peduncle more than 30 cm long; petioles prominently 3–8-ribbed abaxially; fewer than 10 flowers visible in either spiral; northern Colombia (Chocó) to Panama ..... *A. concolor* K. Krause

109b. Peduncle more than 5× longer than petiole.
182a. Cataphylls hook-shaped or cucullate.
183a. Species occurring in the Amazon basin and on eastern slopes of Andes.
184a. Inflorescence erect-spreading; leaf blades usually matte on upper surface when fresh; on eastern slopes of Andes in Colombia and Ecuador; mostly above 440 m ..... *A. harlingianum* Croat
184b. Inflorescence pendent to spreading-pendent; leaf blades semiglossy on upper surface when fresh; in western and northern Amazonia; below 350 m.
185a. Peduncle 5–6× longer than petiole, 3–4 mm diam.; inflorescence strictly pendent; Amazonas and Bolívar, Venezuela ..... *A. cataniapoense* Croat
185b. Peduncle 4–12× longer than petiole, 6–11 mm diam.; inflorescence spreading to spreading-pendent; upper Amazon basin, Brazil (Amazonas), Loreto, Peru and adjacent Colombia and Ecuador ..... *A. loretense* Croat
183b. Species occurring in northern Colombia and coastal Ecuador.

186a. Cataphylls hook-shaped, lanceolate; sea level to 400 m ..... *A. asplundii* Croat
186b. Cataphylls cucullate.
187a. Spadix pale lavender, glaucous; inflorescence usually pendent; petioles rounded abaxially; leaf blades with slightly undulate margins; northern Colombia to Mexico; humid to wet regions, sea level to 1,600 m ..... *A. salviniae* Hemsley
187b. Spadix reddish to violet-purple not glaucous; inflorescence usually erect-spreading; petioles usually 1–4-ribbed abaxially; leaf blades with usually strongly undulate margins; dry coastal Ecuador; sea level to 890 m ..... *A. barclayanum*
182b. Cataphylls straight, lanceolate.
188a. Leaf blades conspicuously quilted, with primary lateral veins conspicuously retrorse-arcuate; Huánuco, Peru; 650–800 m ..... *A. reflexinervium* Croat
188b. Leaf blades not quilted, with primary lateral veins ascending.
189a. Leaf blades usually with conspicuous glandular punctations (at least abaxially).
190a. Leaf blades rounded to subtruncate at base, mostly drying greenish; stipe 15–40 mm long; southeastern Colombia, Amazonas and Bolívar in Venezuela; 75–380 m ..... *A. bonplandii* Bunting subsp. *cuatrecasii* Croat
190b. Leaf blades attenuate to acute or obtuse at base, mostly drying brown or yellowish; stipe 1–20 mm long.
191a. Leaf blades usually elliptic to broadly elliptic; southeastern Colombia, southern Venezuela, northern Brazil; mostly below 500 m.
192a. Blades less than 10 cm wide; petioles less than 6.5 cm long, sheathed to midway; blade surfaces with reticulate veins drying prominently raised ..... *A. vinillense* Bunting
192b. Blades more than 15 cm wide; petioles more than 10 cm long, sheathed no more than ⅓ their length; blade surfaces with reticulate veins scarcely or not at all evident when dried ..... *A. bonplandii* Bunting subsp. *bonplandii*
191b. Leaf blades usually oblanceolate to obovate; Surinam and southern Venezuela; 400–1,500 m ..... *A. bonplandii* Bunting subsp. *guayanum* (Bunting) Croat
189b. Leaf blades without conspicuous glandular punctations.
193a. Spathe withered and turning yellow at anthesis; Trinidad to Brazil (Amapá); less than 500 m ..... *A. jenmanii* Engl.
193b. Spathe green to purplish, not withered at anthesis.
194a. Leaf blades oblong-linear, less than 7 cm wide; dry coastal Ecuador ..... *A. linguifolium* Engl.
194b. Leaf blades mostly oblanceolate to elliptic or ovate-elliptic, more than 7 cm wide.
195a. Primary lateral veins 10–26 per side.
196a. Peduncle more than 6× longer than petioles.
197a. Blades ovate-elliptic, rounded to broadly obtuse at base; Serranía de Huanchaca in eastern Bolivia; 750 m ..... *A. atropurpureum* R. Schultes & Maguire var. *thomasii* Croat
197b. Blades oblanceolate to obovate, acute to attenuate at base; Guiana Highlands or northern Antioquia.
198a. Spadix sessile; spathe less than 9 cm long, less than 1.5 cm wide; Antioquia, Colombia; 300–750 m ..... *A. anorianum* Croat
198b. Spadix stipitate 1.5–2.5 cm; spathe more than 9 cm long, more than 1.5 cm wide; Kaieteur Plateau, Guyana; 470 m ..... *A. cowanii* Croat
196b. Peduncle mostly less than 6× longer than petioles.
199a. Spadix less than 20× longer than thick at anthesis; Ecuador to southern Peru; 950–2,760 m ..... *A. dombeyanum* Brongn. ex Schott
199b. Spadix more than 20× longer than thick at anthesis.
200a. Leaf blades drying subcoriaceous and yellowish brown to green; coastal Ecuador; sea level to 400 m ..... *A. asplundii* Croat

200b. Leaf blades drying coriaceous and dark brown; eastern slopes of Andes in Colombia and Ecuador; 400–1,800 m ..... *A. harlingianum* Croat

195b. Primary lateral veins mostly 4–10 per side.

201a. Leaf blades drying grayish to grayish brown; spadix more than 40× longer than thick; Vaupés and Amazonas in Colombia, adjacent Peru; 130–250 m ..... *A. vaupesianum* Croat

201b. Leaf blades drying mostly green, yellow-green to brownish; spadix less than 40× longer than thick.

202a. Petioles mostly narrowly and deeply sulcate with blunt margins adaxially, rounded abaxially.

203a. Spathe usually spreading-ascending, coriaceous, conspicuously decurrent on peduncle; Rio de Janeiro and Espírito Santo, Brazil .. *A. solitarium* (Vell. Conc.) Schott

203b. Spathe usually reflexed, subcoriaceous, not conspicuously decurrent on peduncle; central Peru; 320–770 m ..... *A. pachylaminum* Croat

202b. Petioles mostly flattened or shallowly sulcate with acute margins adaxially, mostly 1–3-ribbed abaxially.

204a. Leaf blades ovate-elliptic; spathe less than 6 cm long; San Martín, Peru ..... *A. basirotundum* Croat

204b. Leaf blades oblanceolate to oblong-oblanceolate; spathe more than 6 cm long; southern Brazil, Bolivia, Paraguay, and northern Argentina; 150–1,700 m ..... *A. paraguayense* Engl. var. *paraguayense*

108b. Spadix greenish to whitish.

205a. Primary lateral veins toward base of leaf blade perpendicular to midrib to retrorse to 130°.

206a. Leaf blades less than 45 cm long; La Paz, Bolivia; 700–900 m ..... *A. paraguayense* Engl. var. *coroicoanum* Croat

206b. Leaf blades more than 50 cm long; central Peru; 500–1,800 m ..... *A. latissimum* Engl.

205b. Primary lateral veins all ascending, not perpendicular or retrorse to the midrib; widespread in South America.

207a. Peduncle less than 3× longer than petiole.

208a. Species of the Amazon basin and drainage system.

209a. Peduncle less than 2× longer than spadix.

210a. Spadix longer than peduncle; infructescence with apical ca. ⅓ withered; cataphyll fibers fine, hairlike, reddish brown; Peru to Bolivia, Paraguay and Brazil; 50–900 m ..... *A. plowmanii* Croat

210b. Spadix shorter than peduncle; infructescence usually not withered in apical ⅓; cataphyll fibers various, usually not fine and hairlike.

211a. Leaf blades mostly less than 4× longer than petioles; spadix more than 20× longer than thick ..... *A. uleanum* Engl. var. *uleanum*

211b. Leaf blades mostly more than 4× longer than petioles; spadix less than 20× longer than thick (mostly much less).

212a. More than 12 flowers visible in either spiral; spadix whitish.

213a. Spathe shorter than spadix; leaf blades less than 18 cm wide, tinged red to purple below; petioles less than 10 cm long.

214a. Leaf blades less than 4× longer than broad; known only from Napo, Ecuador; 200 m ..... *A. superbum* Madison subsp. *superbum*

214b. Leaf blades more than 4× longer than broad; known only from Río Cenepa area, Amazonas, Peru; 200–300 m ..... *A. superbum* Madison subsp. *brentberlinii* Croat

213b. Spathe longer than spadix; leaf blades more than 18 cm wide, not tinged red or purple; petioles

more than 10 cm long; Acre, Brazil and adjacent Peru and Colombia; less than 300 m ..... *A. galactospadix* Croat

212b. Mostly fewer than 12 flowers visible in either spiral; spadix mostly greenish.

215a. Spadix appearing glaucous; Madre de Dios, Peru; 700 m ..... *A. manuanum* Croat

215b. Spadix not appearing glaucous.

216a. Cataphylls persisting as an intact skeleton of fine, pale fibers; primary lateral veins conspicuously orange below on drying; peduncle and spadix erect; widespread in western Amazonia; below 500 m ..... *A. ernestii* Engl. var. *ernestii*

216b. Cataphylls persisting semi-intact, brown; primary lateral veins not drying orange; peduncle spreading, spadix erect; Pastaza, Ecuador; ca. 1,000 m ..... *A. curtispadix* Croat

209b. Peduncle more than 2× (mostly more than 3×) longer than spadix.

217a. Spadix usually appearing glaucous, or if not appearing glaucous, then cataphylls persisting as an intact network of fine, pale fibers and primary lateral veins drying conspicuously orange on lower surface; epiphytic in moist to wet forest life zones; lowland Amazonia.

218a. Cataphylls persisting as an intact network of fine, pale fibers; leaf blades usually drying greenish, with primary lateral veins usually drying conspicuously orange on lower surface; spadix not appearing glaucous; widespread in western Amazonia; mostly below 500 m ..... *A. ernestii* Engl. var. *ernestii*

218b. Cataphylls persisting semi-intact, brown; leaf blades drying brown, with primary lateral veins not drying orange.

219a. Leaf blades coriaceous, narrowly oblong-elliptic, to 9.5 cm wide, broadest at the middle, drying reddish brown with the tertiary veins prominulous on both surfaces; known only from Napo, Ecuador; 600 m ..... *A. tenaense* Croat

219b. Leaf blades subcoriaceous, usually oblanceolate and broadest well above the middle or rarely elliptic to broadly elliptic in *A. uleanum* var. *nanayense* (if elliptic then usually 11–16 cm wide), drying greenish to grayish green to brown, but not reddish brown, with tertiary veins not prominulous (or at least never on the upper surface).

220a. More than 6 flowers visible in either spiral; western Amazonia; below 550 m ..... *A. uleanum* Engl. var. *uleanum*

220b. Fewer than 6 flowers visible in either spiral; Loreto, Peru, 100–160 m ..... *A. uleanum* Engl. var. *nanayense* Croat

217b. Spadix sometimes pale but not appearing glaucous; usually terrestrial or epilithic in mostly drier life zones.

221a. Leaf blades glandular-punctate on lower surface.

222a. Leaf blades less than 5 cm wide, less than 16 cm long; spadix with stipe less than 5 cm long; Surinam ..... *A. maguirei* A. Hawkes

222b. Leaf blades more than 5 cm wide, more than 16 cm long (usually more than 25 cm); spadix with stipe more than 5 mm long ..... *A. bonplandii* Bunting subsp. *cuatrecasii* Croat

221b. Leaf blades not glandular-punctate on lower surface.

223a. Leaf blades mostly more than 5× longer than broad.

224a. Petioles flat to slightly convex adaxially, rounded abaxially; San Martín, Peru; 130–750 m ..... *A. llewelynii* Croat

224b. Petioles with prominent medial rib adaxially, 1–3-ribbed abaxially; southern Brazil, Paraguay, Bolivia, and northern Argentina; 150–1,700 m ..... *A. paraguayense* Engl. var. *paraguayense*

223b. Leaf blades less than 5× longer than broad.

225a. Stem erect; peduncle more than 2× longer than petioles; San Martín, Peru; 360–700 m ..... *A. tarapotense* Engl.

225b. Stem usually horizontal, creeping; peduncle mostly less than 2× longer than petioles; Brazil in Mato Grosso, Goiás, Pará, and Rondônia ..... *A. lindmanianum* Engl.

208b. Species of central and northern Colombia, Venezuela, southeastern Brazil, not occurring in the Amazon basin.

226a. Primary lateral veins departing midrib at 70–90° angle; cataphylls hook-shaped; central Colombia; 900–1,750 m ..... *A. caucavallense* Croat

226b. Primary lateral veins departing midrib at 30–70° angle; cataphylls straight.

227a. Leaf blades with margins prominently undulate; spadix often broadest near apex; eastern and southeastern Brazil; sea level to 1,300 m ..... *A. affine* Schott

227b. Leaf blades with margins not prominently undulate; spadix broadest near base.

228a. Leaf blades with pale raphides visible at low magnification on drying; spathe 2–6 cm long; spadix 4–12 cm long; northern Venezuela, Curaçao; sea level to 600 m ..... *A. wagenerianum* K. Koch & Bouché

228b. Leaf blades without pale raphides visible at low magnification on drying; spathe 8.0–12.5 cm long; spadix 12–33 cm long, northern Venezuela, northwestern Colombia, Curaçao; sea level to 1,800 m ..... *A. crassinervium* (Jacq.) Schott

207b. Peduncle ≥3× longer than petiole.

229a. Cataphylls cucullate or hooked.

230a. Cataphylls hook-shaped and lanceolate; Colombia; 900–1,750 m ..... *A. caucavallense* Croat

230b. Cataphylls cucullate, moderately broad, not at all lanceolate.

231a. Spadix pale lavender at anthesis, glaucous; inflorescence usually pendent; petioles rounded abaxially; leaf blades with slightly undulate margins; northern Colombia to Mexico; humid to wet regions, sea level to 1,600 m ..... *A. salviniae* Hemsley

231b. Spadix reddish to violet-purple, not glaucous; inflorescence usually erect-spreading; petioles usually 1–4-ribbed abaxially, leaf blades with usually strongly undulate margins; dry coastal Ecuador and Peru; sea level to 890 m ..... *A. barclayanum* Engl.

229b. Cataphylls straight, lanceolate.

232a. Species of the Amazon basin and drainage system.

233a. Spadix longer than peduncle; infructescence with apical ca. ⅓ withered; cataphyll fibers fine, hairlike, reddish brown; Peru to Bolivia, Paraguay, and Brazil; 50–900 m ..... *A. plowmanii* Croat

233b.. Spadix shorter than peduncle; infructescence not withered in apical ca. ⅓; cataphyll fibers various, usually not fine and hairlike.

234a. Spadix appearing glaucous.

235a. More than 6 flowers visible in either spiral; western Amazonia; below 550 m ..... *A. uleanum* Engl. var. *uleanum*

235b. Fewer than 6 flowers visible in either spiral; Loreto, Peru; 100–160 m ..... *A. uleanum* Engl. var. *nanayense* Croat

234b. Spadix not appearing glaucous.

236a. Leaf blades glandular-punctate on lower surface.

237a. Leaf blades less than 5 cm wide, less than 16 cm long; Surinam ..... *A. maguirei* A. Hawkes

237b. Leaf blades more than 5 cm wide, more than 16 cm long.

238a. Leaf blades mostly rounded to subtruncate at base, mostly drying greenish; stipe 15–40 mm long; southeastern Colombia, southern Venezuela; 75–380 m ..... *A. bonplandii* Bunting subsp. *cuatrecasii* Croat

238b. Leaf blades attenuate to acute or obtuse at base, mostly drying brownish or yellowish; stipe 1–20 mm long.

239a. Primary lateral veins steeply ascending, departing midrib at less than 40° angle; known only from Cerro Aratitiyope, Amazonas, Venezuela; 990 m ..... *A. xanthoneurum* Bunting

239b. Primary lateral veins not steeply ascending, departing midrib at 40° or more angle; Surinam, southern Venezuela; 400–1,400 m.

240a. Blades less than 10 cm wide; petioles sheathed to midway; blade surfaces with reticulate veins, drying prominently raised ..... *A. vinillense* Bunting

240b. Blades more than 10 cm wide; blade surfaces with reticulate veins scarcely or not at all raised when dried ..... *A. bonplandii* Bunting subsp. *guayanum* (Bunting) Croat

236b. Leaf blades not glandular-punctate on lower surface.

241a. Cataphylls persisting as an intact network of fine, pale fibers; primary lateral veins often drying conspicuously orange below; western Amazonia; mostly below 500 m *A. ernestii* Engl. var. *ernestii*

241b. Cataphylls persisting semi-intact and brown; primary lateral veins not drying orange below.

242a. Primary lateral veins more than 10 per side.

243a. Spadix more than 20× longer than thick; leaf blades more than 5× longer than broad; known only from the Serranía de Cutucú, Ecuador; 1,300 m *A. bushii* Croat

243b. Spadix less than 20× longer than thick; leaf blades less than 5× longer than broad; Ecuador to southern Peru; 950–2,760 m ..... *A. dombeyanum* Brongn. ex Schott

242b. Primary lateral veins fewer than 10 per side.

244a. Leaf blades more than 3× longer than broad, with prominently undulate margins; southern Brazil, Bolivia, Paraguay, and northern Argentina; 150–950 m ..... *A. paraguayense* Engl. var. *paraguayense*

244b. Leaf blades less than 3× longer than broad, with slightly undulate margins; San Martín, Peru; 360–700 m ..... *A. tarapotense* Engl.

232b. Species of central and northern Colombia, northern Venezuela, southeastern Brazil, and not occurring in the Amazon basin or drainage system.

245a. Spathe more than 10× longer than broad; spadix bluish green and appearing glaucous; central Colombia; 500–2,100 m ..... *A. glaucospadix* Croat

245b. Spathe 1.6–6× longer than broad; spadix not bluish green or appearing glaucous.

246a. Leaf blades with margins prominently undulate; spadix often broadest near apex; eastern and southeastern Brazil; sea level to 1,300 m ..... *A. affine* Schott

246b. Leaf blades with margins not prominently undulate; spadix broadest near base.

247a. Leaf blades with pale raphides visible at low magnification on drying; spathe 2–6 cm long; spadix 4–12 cm long; northern Venezuela, Curaçao; sea level to 600 m ..... *A. wagenerianum* K. Koch & Bouché

247b. Leaf blades without pale raphides visible at low magnification on drying; spathe 8–12.5 cm long; spadix 12–33 cm long; northern Venezuela; northwestern Colombia; Curaçao; sea level to 1,800 m ..... *A. crassinervium* (Jacq.) Schott

Anthurium acutifolium Engl., Bot. Jahrb. Syst. 25: 365. 1898.

a. Anthurium acutifolium var. **acutifolium**. TYPE: Costa Rica. Puntarenas: Río Hakum, Buenos Aires (SE of San Isidro del General), elev. 250 m, *Pittier 6539* (lectotype, B; isolectotypes, BR, CR). Figures 23, 27.

Anthurium scopulicola Standley & L. O. Williams, Ceiba 3: 105. 1952. TYPE: Costa Rica. Puntarenas: vic. Palmar Norte, near sea level, *P. Allen 5788* (holotype, EAP; isotype, F).

Terrestrial or often epilithic; stem 1 cm diam.; roots descending, greenish, smooth to velutinous, elongate, blunt, 2–4 mm diam.; cataphylls subcoriaceous, lanceolate, 6–10 cm long, narrowly rounded to obtuse at apex with a subapical apiculum, dark green, drying dark tan, persisting semiintact, then as linear fibers, eventually deciduous. *Leaves* erect to spreading, occasionally pendent; petioles (2)6–22 cm long, (3)6–9 mm diam., sharply D-shaped to subquadrangular, flattened to broadly sulcate with the margins sharply raised adaxially, sharply 3-ribbed abaxially, surface sparsely pale-speckled; geniculum slightly thicker than petiole, 1.4–2.5 cm long; blades subcoriaceous, elliptic to oblanceolate to broadly oblanceolate, gradually acuminate at apex (the acumen apiculate), attenuate to narrowly acute at base, (11)25–62 cm long, (3.5)5.5–27 cm wide, broadest at or above the middle, the margins weakly undulate; both surfaces semiglossy to matte, medium green above, paler below, drying greenish to greenish brown, matte; midrib flat at base, becoming acutely raised toward the apex above, sharply 2-ribbed at base, becoming sharply raised toward the apex below, paler than surface; primary lateral veins 8–12 per side, departing midrib at 40–45° angle, broadly arcuate to straight, acutely raised above, convexly raised below; tertiary veins weakly raised to sunken above, raised and darker than surface below; reticulate veins weakly visible above, obscure below; collective vein arising from about the middle of the blade or near the apex, sunken above, raised below, equally as prominent as primary lateral veins, 3–5 mm from margin. *Inflorescences* erect to erect-spreading; peduncle (17)24–53 cm long, 3–5 mm diam., 3–6 × as long as petiole, angular; spathe reflexed to reflexed-spreading, subcoriaceous, green, linear-lanceolate, 5–12 cm long, 0.6–1.1 cm wide, broadest just above the base, acuminate at apex (the acumen inrolled); spadix green to white to yellow, sometimes tinged with red-violet, sessile, long-tapered, rarely stipitate, to 2 cm, occasionally cylindroid, (4)7–16 cm long, 6–8 mm diam. near base, 3–4 mm diam. near apex; flowers square to rhombic, 1.9–3.4 mm long, 1.7–2.7 mm wide, the sides smoothly to weakly and jaggedly sigmoid; 5–6 flowers visible in principal spiral, 5–7 in alternate spiral; lateral tepals (0.5)1–1.7 mm wide, the inner margins straight, the outer margins 2–3-sided; stigma ellipsoid, 0.3–0.5 mm long; stamens held above tepals in a circle around the pistil, persisting; anthers 0.4–0.5 mm long, 0.6–0.8 mm wide; thecae oblong-ovoid, divaricate. *Infructescence* 1 cm diam., bearing berries in the lower part of the spadix; berries greenish yellow, obovoid to globose, rounded to somewhat mammilliform at apex, 3.8–4.7 mm long, 3.8–4 mm diam.; seeds 2 per berry, yellow-orange, oblong-ovoid, flattened dorsally, 2.9–3.5 mm long, 1.8–2.3 mm diam., 1.5–2 mm thick.

This species is known from Costa Rica and Panama principally on the Pacific slope in tropical moist, premontane wet, and tropical wet forest life zones, mostly from sea level to 900 m (rarely to 1,500 m). The species has been collected in Panama on the Burica Peninsula in Chiriquí Province. There are two varieties. The typical variety occurs throughout the range of the species, whereas the variety *herrerae* is restricted to drier parts of tropical moist forest.

Anthurium acutifolium var. *acutifolium* is distinguished by its terrestrial or epilithic habit, by its thin, green-drying, oblanceolate to broadly lanceolate leaf blades that are attenuate at the base, by its slender, long-tapered, usually green to yellowish spadix, and by its greenish yellow berries.

It is similar vegetatively to *A. consobrinum*, but does not have the early-emergent pistils characteristic of that species. See variety *herrerae* for comparison with that species.

COSTA RICA. PUNTARENAS: cabecera del Bkis, *Pittier 11129* (BR, CR, US); Boruca, *Pittier 4656* (BR); Buenos Aires, *Pittier 6539* (BR); Río Cañas–Buenos Aires, *Pittier 3862* (BR); Buenos Aires, Ujarrás, 300 m, *Ocampo 2818* (MO, CR); Las Cruces–Villa Neily, Fila de Cal, 500–600 m, *Gómez 19633* (MO, CR); Mellizas, 1,500 m, 8°54′N, 82°46′W, *Romero & Fallas 7* (CM, CR, MO); along road to microwave tower above Golfito, 90 m, *Croat 67615* (MO); Palmar Norte, *Croat 32962* (MO); Refugio de Fauna Silvestre, Peñas Blancas de Esperza, 10°7′50″N, 84°40′25″W, 1,000–1,400 m, *Herrera et al. 280* (B, CR, K, MO); W of Rincón de Osa, along abandoned "high road," 250–540 m, 8°42′N, 83°31′W, *Croat & Grayum 59853* (MO); Burica Peninsula, S of Puerto Armuelles, Quebrada Macho, 100–200 m, *Croat 22127* (F, K, MO); Osa Peninsula at Sirena, *Liesner 2921* (MO); Quebrada Palito, *Croat 22614* (MO). SAN JOSÉ: Quebrada Micos, 8.5 km W of Ciudad Colón, 600 m, 9°55.5′N, 83°17.5′W, *Grayum & Sleeper 6098* (B, CR, K, M, MO); 700 m, *Burger et al. 11938* (F, MO); El General basin, *Skutch 4749* (MO); Pacaca, *Pittier 4099* (BR); El Rodeo, *Hun-*

newell 16560 (GH); 800 m, 9°55′N, 84°16′W, *Barringer & Christenson 3653* (MO); vic. Santa Ana, *Burger & Liesner 7171* (MO), *Taylor 17387* (NY, US); Cerro Turrubares, Puriscal, *Jiménez 628* (US); Río del General, S of bridge over river, *Harmon & Fuentes 6210* (UMO); Río Uruca near Santa Ana, 900 m, *Burger & Liesner 7172* (MO). PANAMA. CHIRIQUÍ: Puerto Armuelles, *Woodson & Schery 904* (MO); W of Puerto Armuelles, *Croat 21938, 21972* (MO), *22474* (MO, PMA, RSA, US), *Liesner 49* (MO, PMA).

b. Anthurium acutifolium var. **herrerae** Croat, var. nov. TYPE: Costa Rica. Puntarenas: Esperanza, Macona, finca of José Herrera C. Miramar, 10°01′40″N, 84°36′33″W, 300–400 m, *Herrera 372* (holotype, MO 3587626; isotypes, CR, K, US). Figure 351.

Planta terrestris: internodia brevia; cataphyllum persistens semi-intactum; petiolus 7–9 cm longus, ca. 3 mm diam., sulcatus; lamina oblongo-elliptica aut elliptica, 21–33.5 cm longa, 7.8–13.5 cm lata, in sicco flavo-viridis; pedunculus 11.5–28.5 cm longus; spatha linearis-lanceolata, viridis, 3.8–5.8 cm longa, 8–10 mm lata; spadix sessilis, luteus, 2.5–5 cm longus.

Based on dried material only. Terrestrial; stem short; internodes short, 1–1.5 cm diam.; roots moderately dense, whitish, woolly-pubescent, to 10 cm long, 5 mm diam.; cataphylls narrowly long-acuminate, 5–6.5 cm long, drying brownish, persisting semi-intact, eventually fibrous at least basally. *Leaves* ± erect; petioles 7–9 cm long, ca. 3 mm diam., ± C-shaped, sulcate adaxially, rounded abaxially; geniculum slightly paler than petiole, less than 1 cm long; blades subcoriaceous, drying moderately thin, oblong-elliptic to elliptic, gradually long-acuminate at apex, attenuate at base, 21–33.5 cm long, 7.8–13.5 cm wide, broadest at middle; both surfaces semiglossy; midrib drying sharply acute above, several-ribbed and paler than surface below; primary lateral veins (9)10–14 per side, departing midrib at 50–55° angle (sometimes to 75° angle nearer the base), moderately straight to the margin, then arcuate toward apex; tertiary veins obscurely visible, some weakly raised below; collected vein usually arising from about the middle of the blade, less commonly from the lower third, flat above, weakly raised below, 3–10 mm from margin. *Inflorescences* erect; peduncle 11.5–28.5 cm long; spathe spreading to reflexed-spreading, green, linear-lanceolate, 3.8–5.8 cm long, 8–10 mm wide, broadest near base, inserted at 45–60° angle on peduncle, narrowly acuminate at apex, narrowly acute at base and weakly decurrent; spadix yellow, sessile, moderately tapered, 2.5–5 cm long, 3–5 mm diam. near base, 2–3 mm diam. near apex; flowers 4-lobed, 2.3–2.5 mm long, 2.2–2.7 mm wide, the sides jaggedly sigmoid, 5–6 flowers visible in principal spiral, 9–10 flowers visible in alternate spiral; tepals semiglossy, lateral tepals 1.3–1.4 mm wide, ± inequilaterally shield-shaped, the inner margins broadly rounded, the outer margins 3–4-sided; pistils not emergent but pushing up against the tepals and inclining their margins upward; stigma 0.4 mm long, 0.3 mm wide, brushlike, with medial separation, weakly exserted; stamens emerging in a regular sequence, the laterals preceding the alternates by ca. 5 spirals, the 3rd stamen preceding the 4th by 3–4 spirals, held tightly aggregated over and obscuring pistil; anthers 0.4–0.5 mm long, 0.7–0.8 mm wide; thecae ovoid, moderately divaricate. Infructescence not seen.

Anthurium acutifolium var. *herrerae* is endemic to Costa Rica, known only from the type collection in a dry area of tropical moist forest at 300–400 m.

It differs from the typical variety by its leaf blades, which are more elliptic and dry yellow-green rather than green. In addition, the dried epidermis of the blades is smooth with a distinct areolate cellular pattern on the upper surface at higher magnifications. In contrast, the typical variety dries dark green and has the surface rough and granular on high magnifications, with no sign of an areolate pattern.

The variety is named in honor of Gerardo Herrera, an outstanding Costa Rican collector working on the Costa Rican Flora Project with B. Hammel and M. Grayum of the Missouri Botanical Garden.

COSTA RICA. PUNTARENAS: Esperanza, Macona, finca of José Herrera C. Miriamar, 300–400 m, 10°01′40″N, 84°36′33″W, *Herrera 372* (CR, K, MO, US).

Anthurium acutissimum Engl., Bot. Jahrb. Syst. 25: 398. 1898. TYPE: Ecuador. San Nicolas, *Sodiro s.n.* (holotype, B). Figures 24, 25.

Anthurium acutissimum var. *maius* Sodiro, Anales Univ. Centr. Ecuador 22, no. 162: 267. 1908. TYPE: Ecuador. *Sodiro s.n.* (n.v.).

Epiphytic, epilithic or terrestrial; stem short, 3–4(10) cm diam.; roots forming a dense mass, descending, drying whitish gray, somewhat pubescent, elongate, 2–4 mm diam.; cataphylls linear-lanceolate, (7)12–17 cm long, linear-elongate, drying brown to reddish brown, persisting semi-intact or as coarse linear fibers or as a reticulum of fibers. *Leaves* spreading to pendent; petioles (7.5)20–50 cm long, 5–12 mm diam., terete to subterete, somewhat flattened adaxially, rounded abaxially,

surface pale-speckled; geniculum flattened, slightly darker and thicker than petiole when dried, 1–2 cm long; blades usually pendent, coriaceous, oblong to oblong-elliptic, acuminate at apex, acute to narrowly acute at base, 60–118 cm long, 7.5–14 cm wide, broadest at or near the middle, the margins flat; upper surface matte, semivelvety, lower surface glossy, both surfaces dark to medium green, drying green to yellowish green, matte; midrib convexly raised, paler than surface above, prominently convex, much paler than surface below; primary lateral veins numerous, more than 25 per side, departing midrib at 50–70° angle, straight to the collective vein, flat and pale above, obscure below, slightly raised above when dried, more so below; interprimary veins moderately numerous, drying almost as conspicuous as primary lateral veins, raised above and below; tertiary veins obscure; collective vein arising from near the base, weakly raised above and below when dried, equally as prominent as primary lateral veins, 4–17 mm from margin. *Inflorescences* spreading to pendent; peduncle 22–64 cm long, (2)3–4 mm diam., equally or to 1.7× as long as petiole, terete; spathe spreading, subcoriaceous, green to green-tinged with purple at margins, oblong-lanceolate, (5.5)8–21 cm long, 1.1–2.4 cm wide, broadest near the base, acuminate at apex (the acumen inrolled, to 25 mm long), acute at base; stipe 7–20 mm long in front, 0–4 mm long in back; spadix green to yellow-green, subsessile, erect, straight to curved, held at 160–180° angle from peduncle, (6.5)10.5–21.5 cm long, (3)6–8 mm diam. near base, (2)4–5 mm diam. near apex, broadest at the base; flowers square to rhombic, 2.2–2.8 mm in both directions, the sides smoothly sigmoid, (3)4–5 flowers visible in principal spiral, 6–9 in alternate spiral; tepals matte, pale-punctate when dried; lateral tepals 1.3–2 mm wide, the inner margins convex, becoming turned up against the pistil, the outer margins 2-sided; pistils emergent, raised, same color as tepals; stigma slitlike, becoming ellipsoid, 0.5–0.8 mm long; stamens emerging from the base, held well above the tepals, persisting, laterals emerging almost to apex before the alternates emerge in basal third, held in a circle around the pistil; filaments white, flattened, exserted, 0.7–1 mm long, 0.6–0.7 mm wide; anthers drying yellowish to brown, 0.5–0.8 mm long, 0.4–0.7 mm wide; thecae oblong, not divaricate. *Infructescence* pendent; spathe persisting, green or withered; spadix ca. 23–30 cm long, 2 cm diam., with berries scattered throughout; berries yellow-orange becoming orange, ovoid to broadly ellipsoid, "hollow" when rehydrated, acute at apex, (6)8.6–9.5 mm long, 4–4.5 mm diam.; pericarp thickened, with some raphide cells; seeds 2 per berry, yellowish, oblong-ovoid, flattened, 3.7–4.8 mm long, 2.3–2.4 mm diam., 1.3–1.6 mm thick, with a transparent, gelatinous appendage at both ends.

A member of series *Multinervia*, *Anthurium acutissimum* is known from the provinces of Pichincha and Los Ríos in Ecuador where it occurs at 650–1,200 m in premontane moist and premontane wet forest life zones.

This species is characterized by its very elongate, mostly pendent, coriaceous, green-drying leaves, which are narrowly acute at the base and long-acuminate at the apex, by its large cataphylls which persist semi-intact as a reticulum of pale fibers, by its long-pedunculate inflorescence which has a tapered, green spadix with anthers exserted on long, whitish filaments and by its ovoid to broadly ellipsoid orange berries.

Anthurium acutissimum is most closely allied to *A. holmnielsenii*, which has generally more erect-spreading leaves, D-shaped petioles, which are sulcate adaxially with prominently raised, sharp margins and broader blades (averaging 5.1 vs. 8.6× longer than broad). Leaves of both species dry dull green and matte.

The label data of *Madison 3826* mention that the plant was "ant inhabited" and that the stem was "massive, 10 cm thick," perhaps owing to its being myrmecophilous; the manner in which it was inhabited by ants is not mentioned, and root mass probably accounts for this exceptional measurement.

ECUADOR. LOS RÍOS: 12 km E of Patricia Pilar, 650 m, *Madison 3826* (QCA, SEL). PICHINCHA: Chiriboga Road, Alluriquín–Chiriboga, 950–1,100 m, *Madison 4198* (originally *2094*) (MO, SEL), *Madison 4075* (MO, SEL); 2–3 km from main Aloag–Sto. Domingo de los Colorados rd., 890–1,010 m, 0°18′13″S, 78°54.5′W, *Croat 56979* (MO, US); 12 km E of Patricia Pilar, 650 m, *Madison 3828* (SEL); Río Pilatón, *Sodiro 20* (B); Quito–Santo Domingo de los Colorados, 44 km E of Santo Domingo, 1,200 m, 0°23′S, 78°50′W, *Hammel & Wilder 16081* (B, MO); Río Pilatón–Río Toachi confluence, 800–900 m, *Madison 4030* (K, QCA, SEL), *Sparre 18453* (S).

Anthurium affine Schott, Oesterr. Bot. Wochenbl. 5: 82. 1855. TYPE: illustrated by Schott Aroideae 465 (lectotype). Figures 26, 28, 29.

Terrestrial; stem short, 1.5–4 cm diam.; roots moderately numerous, descending to spreading, greenish, smooth to weakly pubescent, thick, moderately elongate, 3–8 mm diam.; cataphylls subcoriaceous, broadly lanceolate, 6–20 cm long, acuminate to narrowly rounded and prominently

apiculate at apex, light green, drying brown, persisting semi-intact, eventually dilacerating into coarse linear fibers. *Leaves* erect to spreading; petioles 5–28 cm long, 7–16 mm diam., U-shaped to quadrangular, shallowly to prominently sulcate, sometimes with a medial rib adaxially, prominently and sharply raised marginally, usually (1)3–5-ribbed, or sometimes rounded abaxially; geniculum thicker and slightly paler than petiole, becoming fissured transversely with age, 1–2.5 cm long; blades moderately coriaceous, obovate to oblanceolate to ± elliptic, obtuse to short-acuminate or rounded at apex (the acumen apiculate), acute to obtuse to rounded or shallowly cordate at base, 33–95 cm long, 10.5–32 cm wide, broadest at or above the middle, the margins markedly undulate; upper surface matte to semiglossy, dark green, lower surface semiglossy to glossy, paler, both surfaces drying olive-green to yellow-green; midrib flat and 1-ribbed at base, becoming obtusely angled toward the apex above, slightly paler than surface, prominently thicker than broad and 2–3-ribbed at base below, becoming convexly raised toward the apex, paler than surface; primary lateral veins 7–14 per side, departing midrib at 40–60° angle, slightly arcuate to the margin, prominently and convexly raised above and below; interprimary veins absent; tertiary veins obscure to weakly sunken above, slightly raised and darker than surface below; reticulate veins not visible to prominulous when dried, collective vein arising from near the apex or absent, less prominent than primary lateral veins when present. *Inflorescences* erect, somewhat shorter than the longest leaves; peduncle 31–78 cm long, 4–15 mm diam., 2–9× as long as petiole, green or green-tinged with purple at apex, subterete; spathe reflexed to recurled, moderately thick, purple to green tinged with purple, ovate to broadly lanceolate, (3.5)5–10 cm long, 1.7–7.5 cm wide, acuminate at apex, acute and usually decurrent to 1–3(6) cm at base; stipe 0.5–5 cm long, 6–18 mm diam., pale green to purple; spadix olive-green to yellowish, cylindroid to clavate, subsessile to long-stipitate, erect, straight, 4.5–17 cm long, 5–15 mm diam. near base, 6–10 mm diam. near apex, broadest near the middle or near the apex; flowers ± square, 1.6–2.2 mm in both directions, the sides straight to sigmoid; 7–14 flowers visible in principal spiral, 4–10 in alternate spiral; tepals slightly roughened, pale-punctulate (when dried); lateral tepals 0.7–1 mm wide, the outer margins 2-sided, the inner margins convex to rounded; stamens emerging in a regular sequence from the base, semi-erect in a tight cluster above the pistil, arching over and obscuring it; anthers 0.5–0.7 mm long, 0.7–0.8 mm wide; thecae somewhat divaricate; pollen creamy. *Infructescence* erect; spadix ca. 2.5 cm diam. (not including exserted berries); berries red to rich purple-maroon or purple-maroon at apex becoming red below, whitish toward the base, obovoid to oblong-ellipsoid, truncate at apex, 7–13 mm long, 4–7 mm diam.; seeds oblanceolate, 5–8 mm long, 2–3 mm diam.

Anthurium affine is found in eastern and southeastern Brazil in the states of Mato Grosso, Minas Gerais, Goiás, Bahia, and Pernambuco from sea level to 1,300 m on rocky slopes, along streams, and in open areas. *Heringer 7801* notes the vegetation type as "cerrado mata ciliar."

This species can be recognized by its large, coriaceous leaf blades, frequently with strongly undulate margins, and its relatively short spadix, which is sometimes broadest near the apex.

Because of its fruit color, spadix shape, and geographical isolation, *A. affine* is not easily confused with any other species.

The species was placed into synonymy with *Anthurium solitarium* by Engler, but that species has an elongate, tapered spadix and an elongate spathe, and is primarily restricted to southern coastal Brazil. Engler's drawings of *A. affine* are, in fact, *A. solitarium*.

Confusion arising from Engler's treatment of *A. affine* as a synonym of *A. solitarium* has permeated subsequent publications and label data in Brazil, Europe, and the United States, where it has been cultivated to a limited extent for many years. To this day, any member of sect. *Pachyneurium* from eastern Brazil is usually called *Anthurium solitarium* in botanical gardens and on herbarium labels, and annotations on the latter reflect the confusion between the two epithets.

Anthurium macedoanum, an unpublished name attributed to A. D. Hawkes, was based on an unusually broad-leaved form of *A. affine* (*Macedo 2185*) from San Vincente in the state of Minas Gerais.

Confusion has also resulted from the Field Museum photograph (FM 11838) of *Glaziou 9040* from Rio de Janeiro. This photograph is actually *A. solitarium*, not *A. affine* as annotated by Engler, nor a type of *A. affine* as suggested by the photograph.

BRAZIL. BAHÍA: *Blanchet 1055* (G); Hwy BA:052, Chapada da Diamantina, E of Morro do Chapeú, 900 m, *Davidse et al. 11902* (K, MO); N of Itapuã, Salvador, 0 m, 12°58′S, 38°23′W, *Plowman & Almeida 10046* (F, K, MO); Mato Grosso–Serra do Rio Contas, N of Vila do Rio do Contas, 980 m, 13°33′S, 41°49′W, *Harley et al. 19973* (K, MO); 3 km N of Milagres, BR-116, *Hatsch-*

bach 45069 (K); Morro do Chapeú, 900 m, *Hatschbach 42428* (K); Mucugê, 2 km along Andaraí road, 850 m, 12°59′S, 41°21′W, *Harley et al. 20615* (K); *Hatschbach 47955* (K); Pasto Guanabara, Faz Morro de Pedra–Itaberaba, *Ferreira 191* (K); Rio do Contas–Livramento, cachoeira near road, *Storr 194* (K); Rio Cumbuca, N of Mucugê on Andaraí Road, 850 m, *Harley 16000* (K, US); Rio Ferro Duido, 19.5 km SE of Morro do Chapeú on BA 052 road to Mundo Novo, 900 m, 11°38′S, 41°02′W, *Harley et al. 19254* (K, MO), *22865* (K); Rio Itapicuru, Jacobina, 450 m, *Martinelli 5143* (RB); Rio Paragucu, Andaraí–Mucugê, BA Mucugê, *Pirani et al. 1625* (K, MO); Serra da Jacobina, Senhor do Bonfim–Juàzeiro, BA 130, 12 km N of Senhor do Bonfim, W of Estiva, 850 m, *Harley 16589* (K); Serra das Almas, NW of Rio de Contas, 1,000–1,200 m, *Mori & Benton 13536* (NY); Serra do Jatobá, Morro do Couro or Morro São Cristóvão, 500–600 m, 12°54′S, 39°52′W, *Harley 19427* (K), *19429* (K, MG, MO). Serra do Rio do Contas, Rio do Contas–Mato Grosso, 12–14 km N of Rio do Contas, 1,200 m, 13°28′S, 41°50′W, *Harley 15196* (K); Serra do Sincorá, 5 km S of Andaraí, road to Mucugê near bridge over Rio Paraguacu, 400 m, 12°50′S, 41°19′W, *Harley et al. 18594* (K, MO); Serra dos Lençois, Seabra–Itabera, 7–10 km, W of Lençois turnoff, by Rio Mucugezinho, 12°28′S, 41°26′W, *Harley 22695* (K); Mpo. Jaguarguara, Jaraguara–Milagras, Rodovia BR116, *Silva et al. 1576* (K); Mpo. Lençois, NW of Lençois, Barro Branco road, 630 m, 12°32′S, 41°20′W, *Lewis et al. 920* (K, MO); Mucugezinho Rodovia BR242, 720–760 m, *Lewis & Carvalho s.n.* (K); Mpo. Livramento do Brumado, Rodovia Liv. do Brumado–Rio do Contas, 600 m, *Mori et al. 12242* (K, NY); Mpo. de Palmeiras, ca. km 250 na Rodovia BR 242, *de Carvalho & Saunders 2966* (NY). GOIÁS: Dianopolis, *Pirani et al. 1965* (K, MO, SPF). MATO GROSSO: cultivated at Floricultura Campineira Hda. Campinas, São Paulo (*Oliveira 1420*), *Hutchinson 8849* (MO). MATO GROSSO DO SUL: Ituiutaba, (Furma?) de São Vicente, *Macedo 1237* (RB), *1910* (RB, UC, US), *2185* (UC, US). MINAS GERAIS: Mpo. Diamantina, Diamantina, 1,200 m, *Martinelli 5900* (RB); Rodovia Guinda–Cons. Mata, *Hatschbach & Kummrow 49742* (MBM, MO); road to Diamantina, SW of Mendanha and Rio Jequiti, 1,150 m, *Anderson 8841* (F, NY, US); NE of Diamantina, on road to Mendanha, 1,300 m, *Irwin et al. 22630* (US); Rio Abaite, Rodovia Brasilia, *Heringer 7801* (MG); Rio Jequiti, E of Diamantina, 790 m, *Irwin et al. 27430* (MO, NY, SEL, US); Mpo. Diamantina, Biribiri, *Hatschbach & Pelada 27550* (K), *27990* (MU), *Zappi et al. 47358* (MO); Joaquim Felício, Serra do Cabral, *Zappi et al. 39756* (MO); 1,160 m, 17°42′S, 44°18′W, *Pirani et al. 2183* (K, MO, SPF). PARAÍBA: *Xavier s.n.* (RB), *42082* (RB); vic. João Pessoa, nos Tubuleiros da Costa, *Xavier 9191* (K). PERNAMBUCO: Tapera, *Pickel 2373* (US); Praia do Guaibu, 35 km S of Recife, 10–30 m, *Tsugaru et al. B-1377* (MO, OOM); Rio Formoso, Horto Florestal de Saltinho, *Falcao et al. 775* (MO, RB).

Anthurium angustilaminatum Engl., Bot. Jahrb. Syst. 25: 411. 1898.

a. Anthurium angustilaminatum subsp. **angustilaminatum.** TYPE: Ecuador. Pichincha: Gualea, *Sodiro s.n.* (holotype, B; isotypes, P, Q). Figure 31.

Anthurium angustilaminatum var. *albidum* Sodiro, Anales Univ. Centr. Ecuador 22(156): 21. 1906. TYPE: Ecuador. Imbabura: Guallupe, *Sodiro s.n.* (n.v.).

Anthurium angustilaminatum var. *brevipes* Sodiro, Anales Univ. Centr. Ecuador 22(156): 21. 1906. TYPE: Ecuador. Imbabura: between Paramba and Guallupe, *Sodiro s.n.* (n.v.).

Anthurium angustilaminatum var. *crassum* Sodiro, Anales Univ. Centr. Ecuador 22(156): 20. 1906. TYPE: Ecuador. Pichincha: Nanegal, *Sodiro s.n.* (n.v.).

Anthurium angustilaminatum var. *gladiatum* Sodiro, Anales Univ. Centr. Ecuador 22(156): 20. 1906. TYPE: Ecuador. Imbabura: between Coajara and Paramba, *Sodiro s.n.* (n.v.).

Based on dried material only. Terrestrial; stem short, 1.8–2.5 cm diam.; roots moderately numerous, grayish brown, puberulent, slender, elongate, 2–3 mm diam.; cataphylls 9.5–20 cm long, acuminate to short-acuminate at apex, light brown, persisting semi-intact as fine linear fibers; petioles 8–15 cm long, 5–8 mm diam., D-shaped to subtriangular, broadly rounded to sulcate adaxially, the margins thin, prominently raised, appearing winged, rounded and acutely to obtusely 1-ribbed abaxially; geniculum slightly thicker than petiole, (0.5)1.5–2 cm long; blades coriaceous, narrowly to broadly oblong-elliptic, acute, sometimes shortly acuminate at apex, acute to narrowly acute (rarely rounded) at base, 40–94 cm long, 6–12 cm wide, broadest at or near the middle, the margins narrowly undulate; upper surface green, slightly paler below, both surfaces matte to semiglossy, yellowish brown, sometimes greenish; midrib convexly raised above, prominently raised and 1-ribbed at base, becoming narrowly acutely raised toward the apex below; primary lateral veins darker than surface, 25–35 per side, departing midrib at 30–55° angle, straight to weakly arcuate to the collective vein, prominently raised above; interprimary veins numerous, almost as conspicuous as primary lateral veins; tertiary veins prominulous; collective vein arising from the base, raised above and below, equally as prominent as primary lateral veins, 5–10 mm from margin. *Inflorescences* apparently spreading; peduncle 15–55 cm long, 5–8 mm diam., 2.2–3.1× as long as petioles, green, sharply angular, rarely terete; spathe erect to reflexed, subcoriaceous, yellowish green, lanceolate to ovate-lanceolate, 5–9 cm long, 1–1.3 cm wide, acuminate at apex (the acumen inrolled), narrowly acute at base; spadix dark purple, cylindroid, subsessile, 6–12 cm long, 5–12 mm diam.; flowers rhombic, 1.9–2.4 mm long, 1.5–2.1 mm wide, 4–6 flowers visible in principal spiral, 9–12 in alternate spiral; tepals minutely papillate, lateral tepals 1.4–2 mm wide, the inner margins straight, sometimes broadly convex, occasionally turned up against the pistil,

the outer margins 2-sided; pistils slightly raised; stigma slitlike, 0.5–0.7 mm long; filaments prominently exserted, holding anthers above tepals, the exserted part 0.5–0.7 mm long; anthers yellow, 0.4–0.5 mm long, 0.5 mm wide; thecae oblong-ovoid, not divaricate. *Infructescence* with spathe persisting; spadix ca. 15 cm long, 1 cm diam.; berries drying 2.5–4 mm diam., probably orange.

A member of series *Multinervia*, *Anthurium angustilaminatum* is comprised of two subspecies, the typical one known only from the slopes north of Volcán Pichincha in Pichincha Province in northern Ecuador, and subsp. *cibuserpentis*, from Cotopaxi and El Oro further to the south. Subspecies *angustilaminatum* occurs in a premontane wet forest life zone at ca. 1,200 m.

The species is distinguished by its coriaceous, oblong-elliptic leaf blades with numerous primary lateral and interprimary veins, and its dark purple spadix.

The typical subspecies appears to be most closely allied to *A. soukupii*, which ranges from southern Ecuador to Bolivia, and is very similar morphologically. *Anthurium angustilaminatum* subsp. *angustilaminatum* occurs on the Pacific slope of Ecuador at ca. 1,200 to 1,600 m in a premontane wet or lower montane moist forest life zones, whereas *A. soukupii* occurs on the other side of the Andes at over 2,000 m in various montane forest life zones. Neither species has been studied in cultivation, and for the present, it is felt that the two taxa should be recognized as distinct based on phytogeography, and that study of further collections can be expected to reveal more definitive morphological features for both species. Both subspecies of *A. angustilaminatum* differ from *A. soukupii* in having short, compact (rather than elongate) stems. The habit is epiphytic in at least subsp. *cibuserpentis*, rather than terrestrial as for *A. soukupii*.

A new subspecies, subsp. *cibuserpentis*, is described in the present paper and is distinguished from the typical subspecies mainly by its smaller overall size and abruptly obtuse to truncate leaf bases. It occurs further to the south in Cotopaxi and El Oro provinces, at higher elevations in drier life zones. Like the typical subspecies, it is known only from the Pacific slope of the Andes in Ecuador.

Three of the four varieties described by Sodiro (1906) were collected in the same area in Imbabura Province, not far from the type locality of var. *crassum* and also the typical subspecies. All collections are from the same life zone. Although the type specimens of all four varieties described by Sodiro have not been seen and probably no longer exist (except for a photograph of the type of var. *crassum*), the differences given by Sodiro are slight, and no key is given to distinguish between the varieties. In view of the fact that Sodiro's species concept was often quite liberal, and that the type of var. *crassum* can scarcely be distinguished from material of the typical variety, it seems best to reduce all four varieties to synonymy.

ECUADOR. PICHINCHA: Gualea, ca. 1,200 m, *Sodiro 18* (B, P); *Sodiro s.n.* (G, MO, SI, US); Parroquia Calacali, Reserva geobotanica del Pululahua, Sta. Rita, 0°05′N, 78°30′W, 1,600 m, *Ceron et al. 4763* (MO, QCNE).

b. Anthurium angustilaminatum subsp. **cibuserpentis** Croat, subsp. nov. TYPE: Ecuador. Cotopaxi: Pilalo, Km 80 on Quevedo–Latacunga road, 2,500 m, *Dodson 15397* (holotype, MO 3247505). Figure 32.

Differt a subsp. typicum petiolo breviori; lamina oblonga, basi rotundata vel truncata, nervis primariis lateralis numerosis.

Based on dried material only. Epiphytic; stem short, ca. 2 cm diam.; roots dense, numerous, ascending to spreading, whitish, velutinous, short, tapered, ca. 3 mm diam.; cataphylls subcoriaceous, to at least 8 cm long, yellowish tan, persisting as fine linear fibers. *Leaves* erect; petioles 3.5–7 cm long, ca. 3–6 mm diam., D-shaped, flattened with the margins raised adaxially, rounded abaxially; geniculum 0.3–1 cm long; blades subcoriaceous, oblong-lanceolate to oblong-elliptic, acute at apex, truncate to narrowly rounded at base, 32–61 cm long, 5–9 cm wide, broadest at or near the middle, the margins slightly undulate; both surfaces matte to semiglossy and yellowish green; midrib convexly raised, becoming acute toward the apex above, higher than broad at base, becoming convexly raised toward apex below; primary lateral veins numerous, to more than 20 per side, departing midrib at 50–70° angle, ± straight to the collective vein, raised above and below; interprimary veins numerous, almost as conspicuous as primary lateral veins; tertiary veins raised; collective vein arising from near the base, equally as prominent as primary lateral veins, 3–8 mm from margin. *Inflorescences* erect; peduncle 17–23 cm long, ca. 3 mm diam., 3.9–4.2× as long as petioles, terete; spathe spreading, subcoriaceous, green, at least 7 cm long, 1–1.5 cm wide, acute at base; spadix (post-anthesis) green, slightly tapered, ca. 8 cm long; flowers apparently ± square, 5–6 flowers visible in principal spiral, 6–9 flowers visible in alternate spiral, lateral tepals 2–2.5 mm wide, the

inner margins ± straight, becoming turned up against pistil, the outer margins 2-sided; stigma ellipsoid, 0.4–0.5 mm long; anthers 0.5–0.6 mm long, 0.5–0.7 mm wide; thecae oblong, slightly divaricate. *Infructescence* erect; spathe persisting and withered or absent; spadix ca. 12 cm long, ca. 1.2 cm diam., with berries scattered throughout; berries greenish (immature), oblong, mammilliform at apex, 5.5–6 mm long, 3.2–3.6 mm diam.; pericarp thickened, with raphide cells present; seeds 2 per berry, orange-brown when dried, ca. 3 mm long, 2.2–2.4 mm diam., ca. 1 mm thick.

Anthurium angustilaminatum subsp. *cibuserpentis* is known from the provinces of El Oro and Cotopaxi in Ecuador, where it occurs at 2,135 to 2,500 m in lower montane moist and lower montane dry and/or montane moist (undeterminable from map) forest life zones.

The subspecies is distinguished by its short petioles and more or less oblong leaf blades with numerous primary lateral veins, which are rather abruptly and shortly rounded to truncate at the base. The color of the spadix at (or even near) anthesis is unknown.

Anthurium angustilaminatum subsp. *cibuserpentis* differs from the typical subspecies principally by its abruptly ending leaf bases and by occurring in drier life zones at higher elevations (2,135–2,500 vs. 1,200–1,500 m) to the south, rather than north, of the equator. The new subspecies is smaller in overall size as well. See discussion under subsp. *angustilaminatum* for distinguishing both subspecies from *A. soukupii*.

The name is taken from "cibus" (Latin, meaning food) and "serpentis" (Latin, meaning snake) in reference to label data stating that the fruits of the plant are eaten by snakes.

ECUADOR. COTOPAXI: Km 80 on road Quevedo–Latacunga, 2,500 m, *Dodson 15397* (MO). EL ORO: Pampa de los Cedros, S of Cerro Chivo–Turco, 2,135–2,285 m, *Steyermark 53764* (US, NY).

Anthurium anorianum Croat, sp. nov. TYPE: Colombia. Antioquia: between Segovia and Cañaverales, vic. Río Bagre, 300 m, *Croat 56757* (holotype, MO 3116672-74). Figures 30, 33, 34

Planta epiphytica; internodia brevia, 2–4 cm diam.; cataphyllum lanceolatum, persistens semi-intactum; petiolus 4–9 cm longus, 9–17 mm diam., obtuse D-formatus, late sulcatus; lamina late oblanceolata, basi attenuata, 36–100 cm longa, (12)20–60 cm lata; spatha lanceolata, 7.5–9(35)cm longa, 1–1.3 cm lata; spadix purpureus, leniter contractus, 14–23 cm longus, 5–6 mm diam.

Epiphytic; stem short, 2–4 cm diam.; roots numerous, very dense, spreading, green to whitish, grayish brown on drying, moderately thick, 6–24 cm long, 3–5 mm diam. when fresh, drying 1–2 mm diam.; cataphylls subcoriaceous, lanceolate, 2–3 cm long, acute at apex, green, drying brown (B & K yellow-red 4/10), persisting semi-intact. *Leaves* spreading; petioles 4–9 cm long, 9–17 mm diam., obtusely D-shaped, broadly convex adaxially with the margins shortly and sharply raised, rounded to 3–5-ribbed abaxially, surface pale-speckled, reddish when young; geniculum thicker and slightly paler than petiole, 1–1.5 cm long, prominently and transversely fissured with age; blades subcoriaceous, broadly oblanceolate, acute to acuminate at apex (the acumen apiculate), attenuate at base, 36–100 cm long, (12)20–60 cm wide, broadest above the middle, the margins broadly and shallowly undulate; both surfaces glossy to semiglossy, medium green above, slightly paler below, drying brown to greenish brown; midrib flat to obtusely raised at base, becoming acutely raised toward the apex and slightly paler than surface above, obtusely raised below and slightly paler than surface, pale short-lineate; primary lateral veins 12–16 per side, departing midrib at 40–55° angle, straight or weakly ascending to the margin, sunken above, prominently convex and slightly paler than surface below; tertiary veins obscure above, prominulous and slightly darker than surface below, drying raised on both surfaces; collective vein arising in upper third or fourth of the blade, sunken above, raised below, less prominent than primary lateral veins, raised above and below on drying, 4–20 mm from margin. *Inflorescences* probably erect-spreading; peduncle 69–105 cm long, 5–15 mm diam. when dried, 6–9× as long as petioles, green, drying brown to pinkish brown, terete; spathe spreading, slightly recurled, subcoriaceous, green, tinged with purple near the apex, lanceolate, 7.5–9(35) cm long,1–1.3 cm wide, broadest near the base, acuminate at apex (the acumen inrolled), acute to almost decurrent at base; stipe 1.5–1.8 mm long in front; spadix purple to dark purple, long-tapered, 14–23 cm long, 5–6 mm diam. near base, 3–4 mm diam. near apex; flowers ± rhombic, 3–3.3 mm long, 2.8–3 mm wide, the sides straight, 4–5 flowers visible in principal spiral, 7–8 in alternate spiral; tepals smooth, pale-punctate, lateral tepals 2.1–2.4 mm wide, the inner margins straight to broadly convex, the outer margins 2-sided; pistils green; stigma ellipsoid, 0.4–0.6 mm long; anthers 0.3–0.4 mm long, 0.4–0.5 mm wide; thecae oblong, not divaricate. *Infructescence* with the spathe persisting withered; spadix (12)18–41(100) cm

long, 1.4–1.6 cm diam., bearing berries in the basal portion only; berries dark red, probably acute at apex, drying 4.8–5.5 mm long, 3–3.2 mm diam.

Anthurium anorianum is endemic to Colombia in the Department of Antioquia at 300–750 m in tropical moist and tropical wet forest life zones. All collections to date have been made from the northern drainage of the Río Canoa.

This species is characterized by its short petioles, its subcoriaceous, broadly oblanceolate leaf blades which are attenuate at the base and acuminate at the apex and dry tan to brownish green, and by its slender, long-tapered, dark red to purplish-brown spadix. Especially distinctive is the usually pinkish coloration of the peduncle and primary lateral veins on drying.

Anthurium anorianum is similar in appearance to *A. vaupesianum*, also from Colombia, with which it shares a slender, long-tapered spadix. *Anthurium vaupesianum* differs in being smaller in overall size, in having obovate leaf blades, and in occurring in the Amazon basin.

The species is named after the Municipio Anorí, where most collections were made.

COLOMBIA. ANTIOQUIA: Río Bagre, Segovia–Cañaverales, 1 km NE of village of El Río, 300 m, 7°10′N, 74°38′W, *Croat 56757* (COL, K, MO, US); Segovia–Antioquia, village of El Río, 750 m, *Renteria et al. 1576* (HUA, MO); Mpo. Anorí, Buenos Aires, Corregimento de Providencia, 500–700 m, *Soejarto 2922* (HUA), *2995* (COL, HUA); Río Anorí, Dos Bocas–Anorí, Buenos Aires, trail along Quebrada Sarmiento, 600 m, *Soejarto et al. 4355* (MO); Mpo. Cáceres, El Doce Baja Cauca, 7°27′N, 75°20′W, *Callejas 210* (HUA); Mpo. Valdivia, Corregimiento Puerto Valdivia, 5 km from Puerto Valdivia at Río Pescado, 410 m, 7°20′N, 75°20′W, *Callejas et al. 3447* (HUA, MO, NY).

Anthurium asplundii Croat, sp. nov. TYPE: Ecuador. Los Ríos: Río Blanco, across river from Villa Hermosa, 3 km S of Sto. Domingo–Esmeraldas hwy. at Km 24, 00°05′S, 79°15′W, *Croat 50688* (holotype, MO 3313109-10; isotypes, K, QCA, US). Figures 8, 10, 35–37, 43.

Planta epiphytica; internodia brevia, 3.5–5 cm diam.; cataphyllum lanceolatum; petiolus 7–15(25) cm longus, ca. 10 mm diam., adaxiale complanatus cum costa mediana, abaxiale rotundus; lamina coriacea-subcoriacea, late oblanceolata-elliptica, acuta apud apicem, acuta usque late rotundata ad vadosa cordata apud basim, (60)90–125 cm longa, 20–34 cm lata; nervis primariis lateralis (11)16–26 utroque. Pedunculus (20)33–60 cm longus; spatha oblongo-lanceolata, viridis, aliquando purpurea tincta, (9)12–30 cm longa, 1–1.7 cm lata; spadix purpureus extendens ad marrinonium, leniter contractus, 12–23 cm longus, 3–6 mm diametro. Baccae ignotae.

Usually epiphytic, sometimes terrestrial; stem to 60 cm long, 3.5–5 cm diam.; roots very dense, spreading-ascending, greenish to white, smooth, ca. 7–15 cm long, ca. 5 mm diam.; cataphylls subcoriaceous, lanceolate, straight or hooked, to 14 cm long, acuminate at apex, drying whitish to reddish brown, persisting as linear fibers. *Leaves* erect-spreading; petioles 7–15(25) cm long, ca. 10 mm diam., sharply D-shaped, somewhat flattened with a medial rib and sharply erect or acute margins adaxially, rounded and sometimes weakly 1–2-ribbed abaxially; geniculum moderately thicker and slightly paler than petiole, 1–3 cm long; blades coriaceous to subcoriaceous, oblanceolate to broadly oblanceolate-elliptic, acute to abruptly and shortly acuminate at apex, acute to broadly rounded or shallowly cordate at base, rarely narrowly acute, (60)90–125 cm long, 20–34 cm wide, broadest above the middle, the margins moderately undulate; upper surface semiglossy, medium green (B & K yellow-green 2/7.5), lower surface weakly glossy, moderately paler; midrib convexly raised to prominently 1-ribbed at base, becoming acutely raised toward the apex above, moderately paler than surface, convexly raised and conspicuously paler than surface below; primary lateral veins (11)16–26 per side, departing midrib at 40–50(60)° angle, straight-ascending to very near the margin, then arcuate, frequently congested at base, convexly raised above, less conspicuously so below, paler than surface; interprimary veins usually present toward the apex and base of the blade; tertiary veins rather obscure above, less so below, drying conspicuously raised on both surfaces; reticulate veins prominulous on drying; collective vein arising from near the apex or absent, rather obscure on both surfaces, to 8 mm from margin. *Inflorescences* erect; peduncle (20)33–60 cm long, 3–5 mm diam., 3–6× as long as petioles, terete; spathe reflexed, subcoriaceous, green, sometimes tinged with purple, oblong-lanceolate, (9)12–30 cm long, 1–1.7 cm wide, broadest near the base, acuminate at apex, obtuse at base; spadix dark to dull purple to maroon, sessile or stipitate to 4 cm, cylindroid, slightly tapered, somewhat curved, held at 30–50° angle from peduncle, 12–23 cm long, 5–6 mm diam. near base, 3–4 mm diam. near apex, broadest at the base; flowers rhombic, 1.2–2.5 mm long, 1.2–1.6 mm wide, the sides smoothly sigmoid; 6–9 flowers visible in principal spiral, 4–5(8) in alternate spiral; tepals muricate; lateral tepals 0.7–1.5 mm wide, the outer margins 2-sided, the inner margins nearly straight to rounded; pistils yellowish when dried; filaments (dried) exserted for 0.2–0.3 mm, 0.3–0.7 mm wide; anthers pinkish, 0.3–0.4

mm long, 0.4–0.5 mm wide; thecae ovate, slightly or prominently divaricate.

Anthurium asplundii is endemic to coastal Ecuador in Esmeraldas, Los Ríos, and Pichincha provinces, where it occurs from near sea level to 400 m in tropical dry, tropical moist, and premontane wet forest life zones.

This species is distinguished by its short petioles, its large, oblanceolate leaf blades which are frequently rounded to subcordate at the base and often dry green (sometimes yellowish brown), and by its purple to maroon, often stipitate spadix.

Though sometimes terrestrial, this species is usually epiphytic and in coastal Ecuador can only be confused with *A. barclayanum*. The latter occurs further to the south in mostly drier life zones, and the more narrowly oblanceolate leaves are held in an open rosette, whereas in *A. asplundii* they may overlap in the lower portion and form a tight "bird's nest" rosette. In addition, the blades of *A. barclayanum* are usually strongly undulate, much more so than in the present species, and the cataphyll is cucullate (vs. lanceolate and straight or hooked in *A. asplundii*). The spadix color of *A. asplundii* is dark purple to maroon, and in *A. barclayanum* it is usually greenish.

A species which is remarkably similar in overall appearance to *A. asplundii* is *A. harlingianum*, from the eastern foothills of the Andes, mostly in Ecuador. It differs mainly in its spadix color (dark salmon-pink to pale violet-purple vs. maroon to dark purple in *A. asplundii*) and in having leaves that dry mostly dark brown rather than greenish. The disjunct distribution suggests that the two are remotely related.

An interesting collection is *Dodson & Embree 13097*, from Borbón in northern Esmeraldas, for which the spadix color is reported as "gray-white." In the dried state it is brown, not dark maroon as in other specimens. It otherwise agrees well with *A. asplundii*. Another somewhat aberrant plant is *Harling 4465*, from the Río Blanco in Pichincha, with the geniculum 3 cm remote from the base of the leaf blade.

The species is named in honor of Erick Asplund, the first Swedish botanist to collect for the Flora of Ecuador project and the first to collect *A. asplundii*, in 1955.

ECUADOR. ESMERALDAS: without locality, less than 300 m, *Cobb 44* (MO); 20 km S of Esmeraldas, Hacienda Guayas, *Sparre 15366* (S); Esmeraldas airport–San Mateo, 4.1 km N of bridge over Río Esmeraldas, near sea level, 0°54′N, 79°38′W, *Croat 55586* (CM, QCA, MO, US, NY); Esmeraldas–Sua, 6.4 km N of Río Sua, 29.4 km SW of jct. with road to Esmeraldas, 40 m, 0°52′N, 79°52′W, *Croat 55598* (MO, QCA); Santo Domingo de los Colorados–Esmeraldas, 62 km N of Quinindé, 80 km SE of Atacames, 270 m, 0°35′N, 79°33′W, *Croat 55580* (MO, QCA, NY, RSA); 8.8 km NW of Quinindé, 270 m, 0°26′N, 79°03′W, *Croat 55554* (MO, QCA); 4.4 km SW of Sua, coastal road, 35.7 km SW of jct. with road to Esmeraldas, near sea level, 0°51′N, 79°53′W, *Croat 55608* (MO, QCA); Limones, sea level, *Christenson 1521* (MO); Río Cayapas, Playa Grande, 2 km SE of San Francisco de Cayapas, *Sparre 18039* (S); Zapallo Grande, 150 m, 78°55′W, 0°49′N, *Kvist & Asanza 40886* (AAU); Río Esmeraldas, opposite Quinindé (Rosa Zárate), *Asplund 16346* (S); Río Santiago, Borbón, 30 m, *Dodson & Embree 13097* (SEL); Río Verde, hill above Businga, 300 m, 1°00′N, 79°30′W, *Juncosa 801* (MO). LOS RÍOS: Río Blanco, Santo Domingo de los Colorados–Esmeraldas, 3 km S of Km 24, across river from Villa Hermosa, 250 m, 0°05′S, 79°15′W, *Croat 50685* (K, MO), *50688* (MO, K, QCA, US), *50693* (B, MO). PICHINCHA: 10 km NW of Santo Domingo de los Colorados, road to Esmeraldas, Rancho Brahman, 400 m, *Sparre 15210* (S); below confluence with Río Toachi, 200 m, *Harling 4465* (S); confluence of Río Napo and Río Pilaton, *Sodiro s.n.* (Q).

Anthurium atropurpureum R. Schultes & Maguire, Bot. Mus. Leafl. Harvard Univ. 16: 60. 1953.

a. **Anthurium atropurpureum** var. **atropurpureum**. TYPE: Colombia. Amazonas: Quebrada Agua Preta, *Black & Schultes 46-375* (holotype, GH). Figures 38, 44.

Terrestrial or rarely epiphytic; stem to 30 cm long, 1.5–2 cm diam.; roots mostly descending, 3–30 cm long, 2–4 mm diam.; cataphylls subcoriaceous to coriaceous, 1–7 cm long, narrowly acute at apex, drying pale brown (B & K yellow 5/2.5), persisting ± intact, sometimes as a reticulum of fibers with the apex remaining intact. *Leaves* ± erect; petioles 2–25 cm long, 2–8 mm diam., bluntly D-shaped or terete to subterete, obtusely or narrowly sulcate, sometimes weakly flattened adaxially, rounded abaxially, surface sometimes pale-speckled; geniculum thicker and paler than petiole, concolorous when dried, becoming fissured transversely with age, occasionally to 2.5 cm remote from the base of the blade, 0.5–1.5 cm long; blades subcoriaceous to coriaceous, mostly elliptic, often narrowly so, acuminate at apex (the acumen flat), attenuate or acute at base, 11–75 cm long, (3)5–14 cm wide, broadest at or near the middle, the margins flat to undulate; upper surface semiglossy to glossy, medium green, lower surface matte to semiglossy, sometimes paler, drying pale green; midrib convexly raised to angular at base, becoming narrowly raised toward the apex above, broadly acute at base below, becoming conspicuously and acutely raised to narrowly raised toward apex, paler than surface when dried; primary lateral veins 5–

11 per side, departing midrib at (30)50–60° angle, mostly arcuate-ascending, rarely straight to the collective vein, raised above, prominently convexly raised below; interprimary veins rarely present, etched above, flat below; tertiary veins visible, usually weakly etched above, prominulous and darker than surface below; collective vein arising from near the base or near the apex, sunken above, raised below, 5–10 mm from margin. *Inflorescences* erect, shorter than or equaling leaves; peduncle (8)15–47.5 cm long, 2–5 mm diam., 1.3–4× as long as petiole, terete; spathe spreading to reflexed, withering at anthesis, subcoriaceous, streaked with raphides when dried, green heavily tinged with purple at margins to purple-red throughout, lanceolate to linear-lanceolate, 2–15 cm long, 0.5–2.2 cm wide, broadest near base, inserted at 90° angle on peduncle, acute to narrowly acute at apex, acute at base; stipe 3–15 mm long in front, 2–8(12) mm long in back; spadix usually deep purple (B & K purple 2/7.5), sometimes maroon to brown, cylindroid to long-tapered, erect, 2–14 cm long, 3–8 mm diam. near base, 2–4 mm diam. near apex, broadest at the base; flowers rhombic or 4-lobed, 1.6–2.2 mm in both directions when fresh, 1.8–2.4 mm in both directions when dried, the sides ± straight or smoothly to jaggedly sigmoid, 4–8(10) flowers visible in either spiral; tepals matte, muricate, weakly to conspicuously and minutely papillate, the papillae maroon (B & K red-purple 2/2.5); tepal surface olive-green (B & K yellow 6/10); lateral tepals 0.6–1.5 mm wide, the inner margins straight to concave, the outer margins straight to weakly 4-sided; pistils emergent, raised, the exposed portion ± square, 0.6–0.7 mm in both directions, dark purple to green tinged with purple; stigma ellipsoid to oblong, 0.5–0.6 mm long, 0.2–0.3 mm wide, papillate, densely brushlike; stamens emerging rapidly from the base, in a ± scattered pattern, the laterals preceding the alternates by ca. 8 spirals, the 3rd stamen preceding the 4th by ca. 2 spirals, held against the pistil; anthers greenish yellow, 0.4–0.6 mm long, 0.5–0.8 mm wide; thecae ellipsoid, slightly divaricate; pollen yellow-orange, creamy when dried. *Infructescence* with spathe withered; spadix 4–13 cm long, the stipe 0–5 cm long; berries dark purple to deep red, globose to ellipsoid, 5–6 mm long, 4–6 mm diam.; pericarp dry, thickened with numerous raphide cells; seeds 2 or frequently 1 per berry, oblong-ellipsoid, 3.6–4.4 mm long, 1.8–2.4 mm diam., 1.2–1.4 mm thick, with a gelatinous appendage.

Anthurium atropurpureum ranges from southern Colombia to Brazil (Acre) and in western Bolivia, at low elevations (100 to 160 m) on white sand soils.

This species is distinguished by its leaf blades, with the tertiary veins conspicuously etched above (when fresh), by its adaxially sulcate petioles, and its purple, scarcely tapered spadix subtended by a purple-tinged spathe that withers at anthesis.

Anthurium atropurpureum is most easily confused with *Anthurium bonplandii*. A general distinction for dried material is the color of the leaf blades: yellowish/brownish and mostly concolorous for *A. bonplandii* (except subsp. *cuatrecasii*) vs. ± green and often bicolorous for *A. atropurpureum*. See further discussion under *A. bonplandii*.

Anthurium atropurpureum comprises three sympatric varieties. *Anthurium atropurpureum* var. *arenicola* is a forest epiphyte or an understory terrestrial herb and greatly exceeds the typical variety in size. Variety *thomasii* is endemic to the Serranía de Huanchaca in Bolivia (see that variety for differences). *Anthurium atropurpureum* var. *atropurpureum* ranges from southern Amazonas Dept. in Colombia to Maynas Province (Dept. Loreto) in Peru, as well as Acre and the eastern edge of Amazonas in Brazil, at low elevations in a tropical moist forest life zone. It is distinguished from var. *arenicola* by its much smaller leaves with the collective veins arising from near the base instead of from the upper ½ and to ⅓ of the blade. The varieties *atropurpureum* and *arenicola* share similar soil preference and geographical ranges, although the former is more often terrestrial.

BRAZIL. ACRE: Cruzeiro do Sul, near airport, *Ramos 136* (INPA). AMAZONAS: Rio Tontantins at Villa Velha, near Rio Solimoes, 2°53′S, 67°50′W, *Daly et al. 4341* (INPA, MO, NY). COLOMBIA. AMAZONAS: Amazonas–Putumayo watersheds, above 100 m, *Schultes 6905* (GH); Agua Preta, *Black & Schultes 46-375* (GH); La Chorrea Río Igara–Parana (affluent of Río Putumayo), *Sastre 3232* (COL). PERU. LORETO: Prov. Maynas, 140 m, *Rimachi 7343* (IBE, MO), *Ruiz & Murphy 188* (AAU, F, IBE, MEXU, MO, TEX); Alpahuayo, Estación IIAP, *Vásquez & Criollo 5759* (M, MO); 130 m, *van der Werff et al. 10212* (MO); Iquitos–Nauta, Km 32, 150 m, 4°10′S, 73°30′W, *Vásquez & Jaramillo 7847* (K, MO, US); 130 m, *Vásquez & Jaramillo 10558* (KRAM, MO); Iquitos, Carretera Quisto Cocha–Varillal, ca. 160 m, *McDaniel et al. 27447* (IBE, MO); Quisto Cocha road, near airport, 120 m, *Gentry & Daly 19118* (F, MO); 12–25 km S of Iquitos, *Croat 18279, 18405, 18183, 18665* (MO); Carretera Quisto Cocha–Nauta, 160–170 m, *McDaniel et al. 27605* (IBE, MO); Iquitos at Peña Negra, *Davidson 3659* (RSA); 100 m, *Ayala 1821* (AMAZ); Iquitos–Santo Tomas, S of Iquitos, *Croat 19104* (CAS, COL, F, MO, NY, RSA, SEL); Varillal, road to Nauta, 130 m, 3°45′S, 73°21′W, *Vásquez & Jaramillo 1197* (K, MO), *1198* (MO, RSA); Roca Fuerte (Momón), 160 m, 3°40′S, 73°30′W, *Vásquez & Jaramillo 5232* (MBM, MO); Carretera de Zungaro Cocha, near Shushana, 160 m, *Ri-*

machi 6566 (IBE, MO); near Villa Angel, 140 m, *Rimachi 5888* (IBE); Iquitos Region, Iquitos, Mishuyacu, 120 m, *Killip & Smith 29887* (NY, US), *Klug 316, 207* (F, NY, US); ca. 120 m, *Revilla 4295* (AMAZ); vic. Quista Cocha, 120–140 m, *Croat 51180* (GH, M, RSA, MO), *Gentry 20719* (MO), *Gentry & Ayala 15510* (MO), *Gentry & Jaramillo 22335* (MO), *McDaniel 13604* (MO); Río Amazonas, Dtto. Yanamono, Quebrada Yanamono, Explorama Camp, 150–180 m, 3°24′S, 72°49′W, *Croat 56927* (DUKE, MO, NY), *61761* (AMAZ, MO); Río Nanay, Picuruyacu, 160 m, *McDaniel & Rimachi 26371* (IBE); 30 km SW of Iquitos, Mishana, Estación Biológica Callicebus, 150 m, *Gentry et al. 15782* (B, MO, S); Mishana, *Rimachi 1239* (IBE); 30 km SW of Iquitos, Mishana, 120–150 m, *Foster 4217* (MO), *Gentry et al. 31671* (BM, K, MO), *36536* (MO, RSA), *Solomon 3548* (MO).

b. Anthurium atropurpureum var. **arenicola** Croat, var. nov. TYPE: Ecuador. Napo: road between Lago Agrio and Río San Miguel, 3 km N of Lago Agrio, 0°5′N, 76°50′W, 450 m, *Croat 50303* (holotype, MO 2828986; isotypes, AAU, B, BM, CAS, CM, COL, G, GH, IBE, INPA, K, NY, QCA, RSA, SEL, US, W). Figures 39, 40–42, 45.

Differt a var. typica pro ratione amplioris et distinctis habitationibus suis; et nervo collective prope basim exorienti.

Terrestrial or epiphytic; stem to 30 cm long, 1–3.5 cm diam.; leaf scars obscured by root mass and cataphylls, 1.5–2 cm wide; roots numerous, dense, mostly descending, uppermost ascending, gray or green, smooth to densely pubescent, elongate, blunt, 5–30 cm long, 3–6 mm diam.; cataphylls moderately thin to subcoriaceous, bluntly 1-ribbed near the apex, 5–12 cm long, narrowly acute to acute at apex, tinged with red, drying tan (B & K yellow-red 7/2.5), persisting with apex remaining intact, eventually deciduous. *Leaves* erect-spreading, rosulate or scattered along stem; petioles 4–63 cm long, 3–12 mm diam., erect, slightly thicker than broad to D-shaped, shallowly sulcate adaxially, sometimes obtusely V-sulcate, the margins moderately sharp, rounded abaxially, the surface pale-speckled, tinged with red near the base; geniculum markedly thicker than petiole, slightly paler, 1–3 cm long; blades coriaceous to subcoriaceous, narrowly to broadly oblanceolate, less often elliptic, acute to abruptly acuminate, sometimes gradually acuminate at apex (the acumen to 4 cm long, inrolled), long-attenuate or rarely acute at base, sometimes making geniculum seem remote, occasionally acute to obtuse, (16)45–80(100) cm long, 8–25(41) cm wide, broadest at or above the middle, the margins undulate; upper surface weakly glossy to glossy, medium green, lower surface semiglossy to matte, only slightly paler and mostly eglandular, rarely weakly pustulate, both surfaces drying green and paler below, matte; midrib flat at base, becoming acute-raised to convexly raised toward the apex above, higher than broad to prominently acute-raised below; primary lateral veins 5–13 per side, departing midrib at (30)40–65(70)° angle, usually weakly arcuate-ascending to the collective vein, sunken to convexly raised above, prominently and convexly raised below, paler than surface; interprimary veins etched above, weakly raised below, prominulous when dried; tertiary veins conspicuously etched above, flat to prominulous below; collective vein arising from about the middle or in the upper ⅓ of blade, sometimes arising in lower ½, sunken above, raised below, flat above when dried; antimarginal vein visible on live plant, running close to margin from the base; 1st collective vein 9–12 mm from margin. *Inflorescences* erect to spreading, shorter than or equaling leaves (rarely longer than leaves); peduncle (12)20–73 cm long, 2–8 mm diam., 1–4× as long as petiole, green to green heavily tinged with purple, terete; spathe spreading to reflexed and recurled or twisted, withering at anthesis, subcoriaceous, matte on both surfaces, pale to medium green, heavily tinged with red-violet, sometimes maroon to purple, lanceolate to narrowly lanceolate, 4–22 cm long, 0.6–2.5 cm wide, broadest near the base, inserted at 45° angle on peduncle, long-acuminate at apex, broadly acute, decurrent to 2 cm at base, the margins meeting at ca. 45° angle; spadix green (B & K yellow 5/7.5) heavily tinged with violet-purple, to dark purple or maroon, cylindroid to tapered, sessile or stipitate to 16 mm, erect, 4–26 cm long, 3–8 mm diam. near base, 3–5 mm diam. near apex, broadest at the base; flowers square to rhombic, 1.5–2.6 mm long, 1–2.5 mm wide, the sides straight to sigmoid, 5–8 flowers visible in principal spiral, 5–10 in alternate spiral; tepals matte, weakly to densely and minutely papillate, muricate, lateral tepals (0.5)0.8–1 mm wide, the inner margins pale, thin, pinkish, straight to weakly convex, the outer margins 2–3-sided; pistils weakly emergent before stamens emerge, ± square, green, developing a maroon tinge, sometimes somewhat papillate; stigma ellipsoid, 0.2–0.6 mm long, depressed medially, lightly or densely papillate, droplets appearing 7–11 days before anthesis; stamens emerging in a regular sequence from the base, lateral stamens followed by alternates in rapid succession (7 days), the laterals preceding the alternates by 5–10 spirals, held over and obscuring pistil, 3rd barely preceding 4th; anthers yellow, 0.2–0.6 mm long, 0.8 mm wide, held

at edge of the pistil, only partially exserted; thecae oblong-ellipsoid, 0.2–0.4 mm wide, not divaricate or only slightly divaricate; pollen yellow fading to cream, faintly sweet- or yeasty-scented. *Infructescence* spreading to pendent; spathe withered or absent; spadix 14–35 cm long, 1–2.5 cm diam., bearing berries in the basal portion only, the stipe to 1.5 cm long.; berries white to greenish white basally, violet-purple in apical ½ (B & K purple 2/7.5), subglobose, rounded at apex, 6–8 mm long, 4–6 mm diam.; pericarp somewhat thickened, with raphide cells; mesocarp with raphides, thickly gelatinous; seeds 1–2 per berry, pale green becoming purple (B & K purple 3/2.5), oblong-ellipsoid, 3–6 mm long, 2–3 mm diam., 1.4–1.6 mm thick, with a basal mucilaginous appendage at radicle end.

Anthurium atropurpureum var. *arenicola* ranges from southern Colombia (Putumayo and Amazonas) to western Brazil (Amazonas, Acre, and western Rondônia), Ecuador (Morona Santiago, Napo, and Pastaza), Peru (Amazonas, Loreto, and Madre de Dios), and Bolivia (La Paz), at 100–560 m. It is principally found in tropical moist forest life zones, in mature forest on white sand soils (hence the name); the variety is both terrestial and epiphytic.

Anthurium atropurpureum var. *arenicola* is distinguished vegetatively by its mostly oblanceolate leaf blades, which dry greenish and often bicolorous and are usually long-attenuate with straight margins toward the base and acuminate at the apex. The spadix may be violet-purple or maroon, or green tinged (usually heavily) with these colors, and the spathe is withered at anthesis.

This variety is distinguished from the typical variety by its larger size and occurrence in the forest understory, commonly as an epiphyte, rather than as a terrestrial plant in open areas. It may be confused with the typical variety and var. *thomasii* (see discussion under both varieties). It may also be confused with *A. bonplandii* subsp. *bonplandii*; see discussion under that subspecies.

Variety *arenicola* is also similar to *A. fendleri*, but differs in having more coriaceous blades when dried, mostly long-attenuate leaf bases and long-acuminate apices, whereas *A. fendleri* is rounded or short-acuminate at the apex and mostly rounded to shortly cordate at the base.

BOLIVIA. LA PAZ: Prov. Iturralde. Río Beni, Luisita, 180 m, 13°05′S, 67°15′W, *Haase 343* (MO). BRAZIL. ACRE: Cruzeiro do Sul, Estrada Alemanha, *Prance et al. 11819* (INPA, NY); near airport, *Monteiro & Damião 315* (INPA); NW of Cruzeiro do Sul toward Barão do Rio Branco, 4 km NW of São Francisco, 150 m, 7°36′S, 72°37′W, *Croat & Rosas 62694* (AAU, BM, CM, INPA, MO, NY); *Mutis 48* (US); Cruzeiro do Sul–Rio Branco, 44 km E of Cruzeiro do Sul, Fazenda da Dona Cabuca, 150 m, 7°38′S, 72°35′W, *Croat 62330* (INPA, MO, NY); vic. airport, 150 m, 7°38′S, 72°36′W, *Croat & Rosas 62642* (CM, INPA, MO, NY). AMAZONAS: Casauari, NW of Rio Jurua, *Silva et al. 392* (NY, US); Rio Aripuana, Nova Prainha, SB20-ZD Point 5, *Mota s.n.* (INPA); Rio Javari, Estiraõ de Equador, *Lleras et al. 17265* (INPA, NY); Paumari, above Atalaia, *Prance et al. 23788* (INPA); Rio Urubu, above Iracema, *Prance et al. 4969* (INPA); Mpo. Humaitá, Humaitá–Porto Velho, Km 60, 08°05′S, 63°W, *Texixeira et al. 187* (INPA, NY); Rio Madeira, Tres Casas, *Krukoff 6549* (NY); Mpo. Novo Aripuanã, BR 230, Rodovia Transamazonica, at km 300 from Humaitá, 4°33′S, 60°40′W, *Ferreira 5711* (INPA, NY); Rio Madeira basin, Rio Livramento, Livramento, *Krukoff 6771* (NY). RIO DE JANEIRO: (cultivated by R. Burle-Marx) San Carlos, *Croat 53698* (CM, MO, GUA, NY). RONDÔNIA: Porto Velho–Ariquemes, 4 km N of Ariquemes, *Croat 53582* (MO); Serra dos Tres Irmãos, opposite Mutumparana, N bank of Rio Madeira, *Prance et al. 5535* (COL, INPA, NY, US). COLOMBIA. AMAZONAS: Río Igara–Paraná, Puerto Buenaventura, *Sastre 2449* (US). PUTUMAYO: Río San Miguel and Sucumbios: Conejo, 300 m, *Schultes 3535* (GH). ECUADOR. MORONA–SANTIAGO: El Centro Shuar Kanhaim, (Cangaimine), Río Kankaim (Cangaime), 20 km WNW of Taisha, 500 m, 77°41′W, 02°20′S, *Shiki RBAE207* (NY). NAPO: Lago Agrio-Baeza, 43 km E of Lago Agrio, km 43, 560 m, 0°07′N, 77°15′W, *Croat 50441* (MO); Lago Agrio–Coca, 69 km S of Lago Agrio ferry crossing over Río Coca, 200 m, *Gentry 12558* (MO); Lago Agrio–Río San Miguel, 3 km N of Lago Agrio, 450 m, 0°05′N, 76°50′W, *Croat 50303* (AAU, B, BM, CAS, CM, COL, DUKE, F, G, GB, GH, IBE, INPA, K, LE, M, MO, NY, OOM, QCA, RSA, SAR, SEL, TEX, US, W); 21.2 km N of Lago Agrio, road near Río San Miguel, 470 m, 0°08′N, 76°50′W, *Croat 50358* (AAU, B, CM, K, KYO, L, LE, MBM, MO, QCA, RSA, SEL, US); Puerto El Carmen de Putumayo–Lago Agrio, 76 km E of Lago Agrio, Tarapoa, 240 m, 0°07′N, 76°23′W, *Croat 58630* (MO); Cantón Aguarico, Parque Nacional Yasuní, Iagunas de Garza Cocha, 200 m, *Cerón & Gallo 5006* (MO, QCNE); Río Aguarico–Coca, 8 km S of Río Aguarico, E of Lago Agrio, *Croat 58514* (CM, MO, QCA); Río Aguarico, 300 m, 0°15′S, 76°21′W, *Brandbyge et al. 33207* (AAU); Cantón Putumayo, Dureño, 500 m, *Plowman et al. 4048* (GH); Santa Cecilia, 220 m, 0°4′S, 76°58′W, *Sparre 13022, 13128* (S); Río Aguarico–Coca, Lago Agrio, S side of lake, 5 km NW of town, 280 m, 0°05′N, 76°55′W, *Croat 58683* (MO), *58687* (K, MO, QCA); Lagunas de Cuyabeno, 300 m, 0°01′S, 76°11′W, *Brandbyge et al. 33975, 36010* (MO, AAU); Reserva de Producción Faunística Cuyabeno, 265 m, *Poulsen 78992* (AAU); S of Laguna Garzacocha, 76°11′W, 00°01′S, *Balslev et al. 84689* (AAU); Laguna Cañangueno, 76°11′W, 00°01′S, *Balslev et al. 84903* (AAU, MO); Río Napo, 20 km downstream from Coca, Laguna Taracoa, 250 m, *Besse et al. 1962* (SEL); SW of Puerto Francisco de Orellana, 300 m, 0°32′S, 77°0′W, *Balslev & Madsen 10621* (AAU); Lago Agrio–Coca, 15 km N of Coca (Francisco de Orellano), 350 m, *Croat 50411* (IBE, MO, P, U); Río Suno, 1 mi. above confluence with Río Napo, 290 m, *Whitmore 860* (K, NY); Coca, Texaco landing strip, 300 m, *Foster 3557* (F, MO); Limoncocha, 240 m, *Madison et al. 5330* (MO, SEL); Río Yasuní,

80 km upriver from Rocafuerte, 225 m, *Foster 3735* (F, MO, QCA); Lagunas Jatun-Cocha, 200 m, *Cerón & Gallo 5145* (MO, QCNE), Cantón Lago Agrio, Dureño, 350 m, 0°2′S, 76°42′W, *Cerón 346* (MO); Reserva Indígena Cofan-Dureño, *Cerón & Cerón 3152* (MO); Estación Biológica Jatún Sacha, Río Napo, 8 km E of Misahuallí, 01°4′S; 77°36′W, 450 m, *Cerón 1729* (MO, QCNE). PASTAZA: Laguna Garzayacu, 250 m, 1°29′S, 76°39′W, *Neill & Palacios 6707* (MO); Río Curaray, Lorocachi, 200 m, 1°38′S, 75°58′W, *Jaramillo et al. 31325* (AAU, MO). PERU. AMAZONAS: Río Santiago, 2–3 km from community of Caterpiza, 65 km N of Pinglo, Quebrada Caterpiza, 200 m, *Huashikat 2216* (MO). LORETO: Río Corrientes, upriver from Tnte. Lopez oil camp, almost at Ecuador border, 280–300 m, *Gentry et al. 18975* (MO); Dtto. Pebas, Río Yaguasyacu, Bora native community of Brillo Nuevo, 150 km ENE of Iquitos, 106 m, 3°0′S, 72°05′W, *Treacy & Alcorn 107* (WIS), *165* (F, WIS); Prov. Loreto, Nauta, 160 m, 4°32′S, 73°35′W, *Vásquez & Jaramillo 5092* (MO, RSA), *5095* (MO, VEN); Prov. Maynas, Dtto. Iquitos, road to Zungaro Cocha, 140–160 m, *Rimachi 5882, 5905, 6352, 7172* (IBE); Carretera Peña Negra, 4 km beyond Quisto Cocha, ca. 150, *McDaniel & Rimachi 25741* (IBE), *Rimachi 6421* (IBE, MO); Nina Rumi, 130 m, *McDaniel et al. 27489* (IBE); Iquitos Region, 17 km SW of Iquitos, *Croat 18393, 18506* (MO), *18460* (MO, USM); Quisto Cocha, 120 m, 3°47′S, 73°24′W, *Croat 51179* (C, K, MISSA, MO, SEL), *51180* (BM, GH, M, MO, US), *51182* (MO), *Rimachi 8086* (IBE); road to Picuruyacu, 160 m, *McDaniel et al. 24770* (MO), *Rimachi 5465* (IBE); Río Itaya, Cahuide, *Vásquez & Jaramillo 5644, 5686* (MO), below mouth of Río Ucayali, 130 m, 4°20′S, 72°30′W, *Gentry et al. 30041* (MO); San Antonio, 150 m, 4°10′S, 73°20′W, *Vásquez & Jaramillo 3537* (MO); Puerto Almendras, 120 m, 3°48′S, 73°25′W, *Croat 19048* (MO), *Croat 51216* (BM, CM, MO, US, W); 12 km SW of Iquitos, *Croat 20093* (MO); 130 m, *van der Werff et al. 9778* (MO); 122 m, 3°48′S, 73°25′W, *Vásquez & Jaramillo 4595, 4949, 6099, 6849, 11485* (MO); 5 km from Río Nanay, *Croat 18560* (F, MO, NY, USM); Iquitos-Nauta, Km 44, 150 m, 4°10′S, 73°20′W, *Vásquez et al. 1942* (MO); Mishana-Río Nanay, Estación Biologica Callicebus, 130 m, 3°55′S, 73°35′W, *Vásquez et al. 643* (MO), *Vásquez & Jaramillo 8934* (MO); Indiana-mouth of Río Napo, Explorama Tourist Camp, Yanamono, 130 m, 3°28′S, 72°48′W, *Croat 61761* (AMAZ, MO), *Gentry et al. 31422, 39695* (MO), *Vásquez et al. 5170, 5179* (MO); Río Momón, *Rimachi 5815* (IBE); Santa Maria de Nanay, Quebrada Yarina, 150 m, 3°55′S, 73°40′W, *Vásquez & Jaramillo 12221* (MO); Río Nanay, Iquitos-Sta. María de Nanay, Maynas, 140 m, 3°52′S, 73°30′W, *Gentry & Emmons 38783* (F, MO), *Gentry et al. 39345* (MO); Iquitos-Sta. María de Nanay, Mishana, *Gentry et al. 28857, 28858, 31715, 26538* (MO), *Gentry & Aronoson 25300* (MO); Río Napo, near Paco Cano, 120 m, *Diaz & Jaramillo 1547* (MO); Altura Tutapisco, 3°02′S, 73°15′W, *Croat 20310* (MO); Explorama Llachapa Camp, Quebrada Sucusari, below Mazán, 140 m, *Gentry et al. 27731* (MO); Quebrada Paparo, 110 m, 3°45′S, 72°55′W, *Vásquez & Jaramillo 11689* (MO); Río Yaguasyacu, tributary of Río Ampiyacu, Brilla Nueva, *Gentry & Revilla 20433* (MO); Prov. Ramón Castilla, Río Ampiyacu, trail from Pucaurquillo, upriver from Pebas, 140 m, 3°15′S, 71°56′W, *Stein et al. 4006* (MO); Prov. Requena, Jenaro Herrera, 170 m, 4°50′S, 73°45′W, *Vásquez et al. 2154, 11865* (MO); 140 m, *van der Werff et al. 10015* (MO). MADRE DE DIOS: serranía across Río Alto Madre de Dios, Pantiacolla, 480–840 m, *Gentry et al. 27357* (MO).

Anthurium atropurpureum var. **thomasii** Croat. var. nov. TYPE: Bolivia. Santa Cruz: Prov. Velasco, Serranía de Huanchaca, Parque Nacional "Prof. Noel Kempff Mercado," 13°59′S, 60°43′W, rocky hills E of airport, ca. 750 m, *Thomas et al. 5696* (holotype, MO 3583031; isotypes, K, LPB, NY, University G. N. Moreno, Santa Cruz), Figure 352.

Differt a var. typico lamina ovato-elliptica, rotundata ad basim.

Terrestrial; stem short; internodes short, to 2 cm diam.; roots densely compacted. *Leaves* erect-spreading; petioles 7–20 cm long, to 6 mm diam. (dried), subterete, sulcate adaxially, rounded abaxially; blades moderately coriaceous, ovate-elliptic, rounded to obtuse and apiculate at apex, rounded to broadly obtuse at base but sometimes ending abruptly on the petiole and weakly decurrent, 35–50 cm long, 15–27 cm wide, broadest at or below middle; both surfaces drying matte to weakly glossy, pale yellowish green to gray-green, inconspicuously pustular but not glandular; midrib convexly raised on both sides; primary lateral veins 6–10 per side, departing midrib at 35–70° angle, at least those near the base of the blade arising at an acute angle with the midrib, arcuate-ascending to margin in a broad curve, most of them merging with the margin above the middle of the blade; interprimary veins lacking; tertiary veins prominulous on both surfaces; collective vein usually lacking, sometimes arising from below the middle of the blade and loop-connecting the primary lateral veins, 12–20 mm from margin. *Inflorescences* ± erect, equaling or much longer than leaves; peduncle 52–73 cm long; spathe spreading to spreading-reflexed, thinly coriaceous, soon drying, green, linear-lanceolate, 6.5–11 cm long, (0.9)1.2–1.6 cm wide, broadest above point of attachment, inserted at ca. 70° angle on peduncle, acuminate at apex, acute at base and sometimes decurrent on the peduncle to 1.3 cm; spadix brownish purple, sessile to subsessile, moderately tapered, erect, 6.5–9.5 cm long, (drying) 5–6 mm diam. near base, 4 mm diam. near apex, broadest at the base; flowers square to rhombic, 1.7–2 mm long, 1.6–1.8 mm wide, the sides straight parallel to spiral, smoothly to jaggedly sigmoid perpendicular to spiral, 9–11 flowers visible in principal spiral; tepals matte, minutely papillate, densely covered with a frostlike grayish coating which

can be scraped off; lateral tepals 1–1.2 mm wide, the inner margins rounded, often turned up on drying, the outer margins 2-sided; pistils not at all emergent, obscured by anthers; stamens emerging in a regular sequence from the base, lateral stamens emerging up to 10 spirals before alternate stamens emerge, the 3rd stamen preceding the 4th by ca. 5 spirals; anthers 0.6 mm long, 0.7 mm wide, contiguous, inclined over pistil; thecae ovoid, moderately divaricate. *Infructescence* to 14 cm long, 1.5 cm diam., bearing berries in the basal portion only; berries purple on upper half, white below, obovoid-ellipsoid, rounded at apex, 6.5–8 mm long, 4–5 mm diam.; seeds 1 per berry, dark brown on rehydration, slightly flattened, 4.5–5 mm long, 3.5 mm diam., lacking any obvious appendage.

Anthurium atropurpureum var. *thomasii* is endemic to the Serranía de Huanchaca near the eastern border of Bolivia, known only from the type specimen collected in Santa Cruz Department in a region of tropical moist forest at ca. 750 m elevation. The type locality is an outlying upland area of the Brazilian shield with "cerrado" and "campo rupestre" vegetation, most closely related to that of adjacent Mato Grosso (W. Thomas, pers. comm.). The population of plants from which the type was collected was growing on steep, dry slopes in a relatively mesic area near a stream in both sunny areas and in partial shade (W. Thomas, pers. comm.).

The taxon is distinguished by its narrowly ovate-elliptic blades which dry pale green and are rounded basally. Also distinctive is the long-pedunculate inflorescence with a lanceolate spathe which is three or more times broader than the purplish spadix. The typical variety as well as the var. *arenicola* are both distinguished from var. *thomasii* by typically having attenuate to narrowly acute blade bases.

The new taxon is named in honor of Wayt Thomas, New York Botanical Garden, who made the only known collection of this taxon and who supplied valuable data on the ecology.

BOLIVIA. SANTA CRUZ: Velasco, Serranía de Huanchaca, Parque Nacional "Prof. Noel Kempff Mercado," 750 m, 13°59′S, 60°43′W, *Thomas 5696* (K, LPB, MO, NY).

Anthurium barclayanum Engl., Pflanzenr. IV 23B(Heft 21): 79. 1905. TYPE: Ecuador. Manabí: Isla Salango, *Barclay 646* (holotype, BM). Figures 14, 46–49, 59.

Terrestrial or epiphytic; stem to 40 cm long, 3–5 cm diam.; roots dense at the nodes, spreading-ascending, green to greenish white, fuzzy, ca. 7 cm long, 4–8 mm diam.; cataphylls subcoriaceous, 3.5–4.5 cm long, cucullate, rounded at apex, drying tan to brown, persisting ± intact or as fine linear fibers. *Leaves* erect-spreading; petioles 5–21 cm long, (5)7–15(20) mm diam., ± D-shaped, flattened or convex with sharp, erect margins and an acute or obtuse medial rib adaxially, obtusely angled, usually 1–4-ribbed abaxially; geniculum slightly paler and thicker than petiole, 1–7 cm long; blades subcoriaceous, narrowly oblong-oblanceolate to oblanceolate-elliptic, obtuse to acute and apiculate at apex, narrowly acute, sometimes abruptly obtuse, less often broadly rounded at base, (40)70–137 cm long, (7)11–32(48) cm wide, broadest above the middle, the margins strongly to moderately undulate; upper surface matte to semiglossy, medium green, lower surface matte to semiglossy, scarcely paler; midrib obtusely raised or flattened with a blunt medial rib at base, becoming acute toward the apex, same color as or paler than surface above, broadly and acutely raised at base, becoming convexly raised toward apex below; primary lateral veins 11–25 per side, departing midrib at 40–60° angle, straight- or arcuate-ascending to the margin, obtusely raised and nearly same color as surface above, convexly raised and paler than surface below; tertiary veins slightly raised, same color as surface above, slightly raised and darker than surface below; collective vein arising from near the apex, prominulous on both surfaces, ca. 5 mm from margin. *Inflorescences* spreading, sometimes erect; peduncle (20)40–80 cm long, (3)5–7 mm diam., 3.5–6(9)× as long as petioles, green to green heavily tinged with maroon, terete; spathe spreading to reflexed-recurled, coriaceous to subcoriaceous, green (sometimes tinged with violet-purple) to dark violet-purple or maroon, narrowly ovate to oblong-lanceolate, (4)7–24 cm long, 0.6–4 cm wide, broadest near the base, inserted at 30–70° angle on peduncle, acuminate at apex (the acumen inrolled), acute to subcordate at base; spadix usually brownish or olive-green to greenish yellow, sometimes reddish to violet-purple, sessile, cylindroid, slightly tapered, erect, usually somewhat curved, held at 140° angle from peduncle, (5)8–18 cm long, 5–10 mm diam. midway, 3.5–5 mm diam. near apex, broadest at the base; flowers 4-lobed, 1.2–2.5 mm long, 1.6–2.5 mm wide, the sides straight to sigmoid, 7–11 flowers visible in principal spiral, 6–7 in alternate spiral; tepals matte, weakly to moderately papillate; lateral tepals 0.8–1.4 mm wide, the inner margins straight to broadly rounded, the outer margins irregularly 3–4-sided; pistils emergent or not, reddish violet

to dark purple or green; stigma linear to elliptic, 0.6–1 mm long; stamens emerging in a regular or scattered pattern, the laterals preceding the alternates by ca. ½ length of the spadix, the 3rd stamen preceding the 4th by ca. 15 spirals, arching over and obscuring pistil; anthers purplish violet to pinkish tan, 0.6–0.8 mm long, 0.8–0.9 mm wide; thecae oblong-ellipsoid to ovoid, slightly divaricate; pollen pale yellow to creamy, fading to white, spicy-scented. *Infructescence* spreading; spadix (6)14–28 cm long, 2 cm diam., greenish when young; mature fruits unknown; berries reddish brown, obovoid, 8–9 mm long, 4–5 mm diam.; seeds 5–6 mm long, 2.5–2.7 mm diam., 1.3–1.5 mm thick, with a gelatinous appendage at each end.

Anthurium barclayanum occurs in coastal Ecuador in El Oro, Manabí, and Guayas provinces, and in adjacent Tumbes Dept., Peru, from sea level to 890 m, in premontane moist, premontane dry, and very dry tropical forest life zones, as well as in tropical desert scrub. It is expected to be in tropical dry forest.

This species is characterized by its large, usually strongly undulate leaf blades, the usually greenish spadix and by its occurrence in dry habitats. *Anthurium asplundii*, its closest ally, occurs in adjacent Esmeraldas and Pichincha provinces in less dry life zones. Another close ally is *A. linguifolium*, which is sympatric with *A. barclayanum* in at least one locality, where *A. barclayanum* is epiphytic and *A. linguifolium* terrestrial in open areas. See those species for distinguishing characters.

In the southern part of its range, in El Oro Province, the spadix color of *A. barclayanum* is sometimes violet-purple, but these plants (e.g., *Croat 50711*, *50712*; *Thompson 362*) otherwise agree well with other specimens. An intergradation with *A. asplundii* (with spadices maroon to purple) is conceivable, but the aberrant specimens of *A. barclayanum* occur in the part of its range furthest from *A. asplundii*, well separated by typical material with greenish spadices.

One collection (*Iltis & Mohr 234*) shows the odd character of having the tepals colored like the pistils, shriveled and very inconspicuous (compared to the pistils) in early fruit, whereas in all other specimens at apparently the same stage (or very near) the tepals are pale and conspicuous and not as shriveled.

ECUADOR. EL ORO: Avenillas–Piñas, 03°40′S, 79°45–55′W, *Thompson 362* (CAS, CM, GH, MO, RSA, UCLA); Machala–Loja, 1 km SE of La Avareada, 18 km NW of Saracay, 80 m, 04°25′S, 79°55′W, *Croat 50711* (C, MO, P, QCA); 25 km SE of jct. to Pinas, 890 m, 04°15′S, 79°45′W, *Croat 50712* (BM, M, MISSA, MO, OOM, QCA); 7.6 km from Tahuir, road to Piedras, 100 m, *Thompson 132* (MO). GUAYAS: Manglaralto–La Rinconada, *Harling et al. 20777* (GB). MANABÍ: Isla Salango, 01°36′S, 80°52′W, *Barclay 646* (BM); Jipijapa–Puerto López, 5 km S of Punta Cayo, 150 m, 01°25′S, 80°42′W, *Croat 50708* (B, CAS, K, M, MBM, MO, NY, RSA, SAR, SEL, US, W); N of San Vicente, farm road E of Hda. Napo (Hotel de la Playa), 50 m, *Croat 50702* (B, CAS, CM, F, GH, IBE, K, MO, OOM, QCA, U), *Iltis & Mohr 234* (WIS, QCA); MANABÍ–GUAYAS: Puerto López–Río Ayampe, 01°33–45′S, 80°40′W, *Thompson 373* (MO, SAR). PERU. TUMBES: Prov. Zarumilla, Dtto. Matapalo, Cerro Tres Picos, El Caucho–Figueroa, 3–4 km on trail from Figueroa, Campo Verde road, 550 m, *Simpson & Schunke 394* (F).

Anthurium basirotundum Croat, sp. nov. TYPE: Peru. San Martín: Tarapoto, above Hotel Turista, 400 m, cultivated at SEL (# 86-1976-2), *Plowman 5980A* (holotype, MO 2727371; isotype, SEL). Figures 50–52.

Internodia brevia, 2–3 cm diam.; cataphyllum lanceolatum, persistens fibris subtilibus et reticulatis; petiolus 5–24 cm longus, 3–5 mm diam., D-formatus aut plus minusve triangulatus, adaxialiter complanatus, marginibus acute elevatis; lamina ovata-elliptica, (15)19–41 cm longa, 6–17 cm lata, basi acuta, obtusa, rotundata vel subcordata; nervis primariis lateralis (3)4–8 utroque. Pedunculus (17)26–36 cm longus; spatha oblonga-lanceolata, 2–6.2 cm longa, 1.2–1.8 cm lata; spadix 3.5–9 cm longus, violaceus ad purpurascens. Bacca ovoidae, 4.5–5 mm longae, vinosae.

Stem to 12 cm long, 2–3 cm diam.; leaf scars obscured by cataphylls, 0.8–1 cm high, 1.4–1.7 cm wide; roots numerous, descending to spreading, green, scurfy, weakly pubescent, slender and elongate, 10–11 cm long, 3–5 cm diam.; cataphylls subcoriaceous, lanceolate, 3–7 cm long, rounded at apex with a subapical apiculum, green tinged reddish, drying tan to brown (B & K yellow 6/5), persisting as a reticulum of fibers with apex remaining intact, eventually deciduous. *Leaves* erect-spreading; petioles 5–24 cm long, 3–5 mm diam., D-shaped to somewhat triangular, flattened, sometimes with a medial rib adaxially, the margins sharply raised, rounded to obtusely 1-ribbed abaxially, surface sometimes minutely pale-speckled; geniculum slightly thicker than petiole, ca. 0.7 cm long; blades subcoriaceous, ovate-elliptic, acute at apex (the acumen slightly inrolled), acute to obtuse to usually semirounded to subcordate (sometimes acute to obtuse) at base, (15)19–41 cm long, 6–17 cm wide, broadest at or below the middle, the margins broadly undulate; both surfaces matte to semi-glossy, dark to medium green above, somewhat paler below, brown to green on drying; midrib acutely raised at base, becoming flat toward the

apex above, prominently convex at base and slightly paler than surface below; primary lateral veins (3)4–8 per side, departing midrib at 45–50° angle, weakly arcuate-ascending, slightly acutely raised above, somewhat convexly raised below; interprimary veins obscure; reticulate veins obscure; collective vein arising from near the base or in the upper ⅓ of blade, weakly sunken above, raised below, 5–10 mm from margin. *Inflorescences* erect to erect-spreading; peduncle (17)26–36 cm long, (2)3–5 mm diam., 1.5–7.7× as long as petioles, green tinged with red-violet or purple, terete, sometimes sulcate; spathe reflexed-spreading or sometimes recurled, subcoriaceous to coriaceous, deep red-violet to dark purple (B & K purple 2/7.5), oblong-lanceolate, 2–6.2 cm long, 1.2–1.8 cm wide, broadest near the base, inserted at 30–35° angle on peduncle, abruptly acuminate to cuspidate at apex (the acumen inrolled), rounded to obtuse at base, the margins meeting at 180° angle; spadix red-violet to violet-purple (B & K purple 2/7.5), tapered to somewhat cylindroid, sessile, erect, straight, 3.5–9 cm long, 5–9 mm diam. near base, 3–4 mm diam. near apex, broadest at the base; flowers ± square to rhombic or 4-lobed, 2.2–3.2 mm long, 2.1–3.5 mm wide, the sides straight to smoothly sigmoid, 5–6 flowers visible in principal spiral, 8–9 in alternate spiral; tepals smooth to weakly papillate, matte, weakly punctate; lateral tepals 1–2 mm wide, the inner margins ± straight to convex, the outer margins 2-sided; pistils emergent, dark red-violet; stigma ellipsoid to linear, 0.5–0.7 mm long, brushlike; stamens emerging in a regular sequence from the base, laterals emerging almost to the apex before alternates emerge; filaments exserted, ca. 0.5 mm, 0.6 mm wide; anthers reddish to purple-violet, 0.4–0.8 mm long, 0.6–1 mm wide, inclined over the pistil; thecae ellipsoid to oblong, 0.3 mm wide, not divaricate; pollen cream-yellow (B & K yellow 9/2.5), fading to white. *Infructescence* with spathe persisting; spadix 4.3 cm long, 0.9 cm diam.; berries deep wine-red, ± ovoid, rounded at apex, 4.5–5 mm long, 3–3.5 mm diam.

Anthurium basirotundum is known only from Peru in San Martín Department in the vicinity of Tarapoto in a tropical dry forest life zone at 400 m.

This species is characterized by its small overall size, leaf blades which are broadest generally below the middle and usually rounded to subcordate at base, and by its long-pedunculate inflorescence with a tapered, red-violet to violet-purple spadix and deep wine-red berries.

Anthurium basirotundum is probably most closely related to *A. tarapotense*, which occurs in the same area. The latter differs mainly in its elliptic-oblanceolate leaf blades which are attenuate to long-attenuate (rarely acute) at the base.

The species is named for the leaf blades, which are usually rounded to subcordate at the base.

PERU. SAN MARTÍN: Tarapoto, above Hotel Turista, 400 m, cultivated at SEL (#81-1976-2), *Plowman 5980A* (MO, SEL).

Anthurium bonplandii Bunting, Acta Bot. Venez. 10: 267–268. 1975.

a. Anthurium bonplandii subsp. **bonplandii**. TYPE: Venezuela. Amazonas: Dept. Atures, Río Orinoco near Siquita, between Isla Castillito and San Fernando de Atabapo, 100–140 m, *Bunting et al. 3676* (holotype, MY). Figures 53–55.

Anthurium atropurpureum var. *apertum* R. E. Schultes, Bot. Mus. Leafl. Harvard Univ. 16: 180. 1951. TYPE: Colombia. Amazonas: Jerijerimo, Río Apaporis, *Schultes 12094* (holotype, GH).

Anthurium bonplandii Bunting subsp. *rionegrense* Bunting, Phytologia 64: 459, figs. 1, 2. 1988. TYPE: Venezuela. Amazonas: Dept. Río Negro: San Carlos de Río Negro, 125 m, *Steyermark & Bunting 102741* (holotype, MO).

Terrestrial, rarely epilithic or epiphytic; stem 10–20 cm long, 1–4 cm diam.; roots descending and spreading, sometimes ascending when epiphytic and forming a globose "ant garden," grayish brown when dried and with raphide cells, reportedly with velamen, 5–28 cm long, drying 3–5 mm diam.; cataphylls subcoriaceous, 2–13 cm long, acute at apex, green, drying pale brown, persisting intact or as weathered fibers, once reported to be deciduous. *Leaves* erect-spreading; petioles (6)10–35 cm long, 3–20 mm diam., D-shaped, often broader than thick, flattened to broadly concave and occasionally with a medial rib adaxially, rounded to 4-ribbed abaxially; geniculum slightly thicker than petiole, 0.5–1.5 cm long, sheathing in lower ⅓ to ⅛ of the petiole; blades coriaceous, elliptic to broadly elliptic, rarely somewhat oblanceolate, acute to acuminate at apex (the acumen ± flat or slightly inrolled), usually acute to attenuate (sometimes barely rounded) at base, (10)30–75(100) cm long, (5)10–30(40) cm wide, broadest at or near the middle, the margins usually flat; upper surface glossy to semiglossy, dark green, lower surface ± matte, paler, usually pustular or glandular-punctate; midrib prominently convex above and below,

somewhat raised on both surfaces when dried, glossy, paler than surface below; primary lateral veins (6)7–10(15) per side, departing midrib at (25)45–70° angle, usually arcuate-ascending to the margin, sometimes loop-connecting (especially in the upper ½ to ⅓ of the blade), raised on both sides; interprimary veins very few, obscure when dried; tertiary veins sunken above, raised on both surfaces when dried; collective vein arising from about the middle to the upper ⅓ of blade, 3–15 mm from margin; antimarginal vein arising from the base and continuous with margin. *Inflorescences* ± erect, equal to, shorter than, or longer than leaves; peduncle (18)30–90 cm long, 2–15 mm diam., 1.5–9(12)× as long as petiole, green, ± terete or slightly flattened on one side; spathe spreading-reflexed to reflexed, subcoriaceous, pale green, often with purple nerves or suffused violet-brown, linear-lanceolate to lanceolate, 5–16 cm long, 0.5–2.5 cm wide, broadest near the base, narrowly acute to acuminate at apex (acumen 10 mm long), decurrent at base; stipe 4–23 mm long in front, 3–20 mm long in back; spadix dark purple to reddish at anthesis, grayish green to brown post-anthesis, mostly cylindroid, slightly tapered at apex, erect, (3)5–15(17) cm long, 1–4(6) mm diam. near apex, 3–9 mm diam. near base; flowers rhombic to 4-lobed, (1.8)2.2–2.8 mm long, (1.6)1.8–2.4 mm wide, the sides ± straight or somewhat jaggedly sigmoid, 3–7(8) flowers visible in principal spiral, 5–7 in alternate spiral; tepals pale-punctate, smooth to minutely papillate; lateral tepals 1.2–1.8 mm wide, the inner margins rounded, the outer margins ± straight, 2-sided; pistils emergent, somewhat papillate; stigma squarish to rounded, 1.2 mm long, depressed medially; lateral stamens preceding the alternates by 6–20 spirals; anthers yellowish white, 0.6–0.8 mm long, 0.7–1 mm wide, inclined over and obscuring the pistil; thecae oblong to somewhat triangular, slightly divaricate. *Infructescence* with spathe withered or absent; spadix (5)8–25(35) cm long, 1–2 cm diam., bearing berries in the basal portion only, stipe 5–15 cm long; berries purple, white at base, obovoid, obtuse-truncate at apex, 5–7 mm long, 5–6 mm diam.; pericarp very thickened, with raphide cells; seeds 1–2 per berry, 4–5 mm long, 2–4 mm diam., with mucilage on one end but hanging on to carpel wall by thick band of fibers.

Anthurium bonplandii is known from sea level to 1,400 m throughout much of the northern Amazon basin, ranging from southeastern Colombia to southern Venezuela and to northern Brazil. It occurs on sandstone rocks of the Guiana shield as well as on granite boulders or granitic outcrops (materials originally underlying the Guiana shield) and on white sand deposited by eroded Guiana sandstone on the lowland plateau of the Tertiary Amazon Lakebed (Guerra, 1959).

This species is recognized by its distinctly long-pedunculate inflorescence (the peduncle typically being 1.5–7× as long as the petioles), by the glandular punctations on the underside of the leaf blade, by the tough, leathery pericarp and meager mesocarp in rehydrated berries, and by the seeds attached to the apical end of the inner carpel wall by a thick strand of fibers running midway from the apex to the base of the fruit.

Anthurium bonplandii may be confused with *A. atropurpureum*, which has leaf blades of similar shape and which also occurs on white sand deposits. The latter differs in having generally smaller, eglandular leaf blades which dry greenish (vs. brownish in *A. bonplandii*), as well as a smaller inflorescence and different berries. The berries of *A. atropurpureum* typically have a soft, pulpy mesocarp on rehydration and lack a fibrous attachment to the carpel wall, having instead a mucilaginous appendage, the typical condition for the section. *Anthurium bonplandii* is also similar to *A. guanchezii*, *A. iramirezae*, *A. lanjouwii*, and *A. xanthoneurum*. See those species for a discussion of the differences.

Anthurium bonplandii is variable in its overall morphology, as well as in ecological preferences. There are three subspecies:

Subspecies *cuatrecasii* ranges across the northern fringe of the Amazon basin from southeastern Colombia to the western half of Amazonas in Venezuela at 75–380 m, primarily on rocks. It differs from the other subspecies in its typically rounded or subtruncated leaf bases, longer peduncles and elongated stipe.

Subspecies *guayanum* occurs in the Guiana Highlands of Venezuela, Guyana, and Surinam, usually above 500 m, and differs from the other subspecies in its generally much larger, prominently dark, glandular-punctate (abaxially) leaf blades.

Anthurium bonplandii subsp. *bonplandii* ranges from southeastern Colombia (Vaupés, Meta, Guainia, and Amazonas) east to Venezuela and Brazil in the middle and upper Río Orinoco Basin, the upper Río Negro, and the Rio Trombetas, and south to the states of Amazonas, Pará, and Roraima in Brazil at usually less than 500 m (rarely to 825 m). It is predominantly terrestrial in sandy areas or, less frequently, is found growing on rocks or in open savanna areas, or in primary forest. In

Brazil, it has been reported from "caatinga" forest or "campina abierta." In Venezuela it occurs mostly in a tropical moist forest life zone. Subspecies *bonplandii* is recognized by its elliptic or rarely oblanceolate leaf blades which are acute at the base, and by its raised, caviform stigma. It is highly variable in size, leaf shape, and in the degree and type of glandlike structures on the lower blade surface. It overlaps geographically with the other two subspecies; see the discussions under the latter for further comments.

Particularly noteworthy in subsp. *bonplandii* are a series of collections from southwestern Venezuela in Amazonas along the upper Río Orinoco Basin and the intervening river system connecting the Río Orinoco with the Río Negro, e.g., the Río Casiquiare (including the Río Yatua, one of its tributaries). These collections are notable for their large size, with blades ranging from 63 to 98 cm long and 30 to 48 cm wide. Despite the fact that these collections differ rather radically from most others, they differ little from the largest plants found in populations around nearby San Carlos de Río Negro, where a wealth of collections from a small area enables a more clear assessment of interpopulational variation. Of these, the largest leaf blades observed were those of *Liesner 3778*, which are 85 cm long and 32 cm wide, with 10 primary lateral veins per side. The smallest plants from this area have blades 28 × 11 cm and only 8 pairs of primary lateral veins per side. These smaller plants differ little from collections made along the Upper Rio Negro in Brazil.

At the western edge of its range, the leaf blades of many collections of subsp. *bonplandii* are typically more narrowly oblong-oblanceolate than elsewhere, being up to 5× longer than broad. On average, blades are 2.6× longer than broad and infrequently are more than 3× longer than broad. The blades of most collections from the upper Rio Negro are 2.5–4× longer than broad, while collections from the middle Rio Negro and the upper Río Orinoco drainage range from 1.7 to 3× longer than broad.

The proportional length of the blade vs. the petiole is highly variable, ranging from only slightly longer to 14.4× longer. Blade shape appears to be in no way correlated with blade size, though the generally more narrowly oblanceolate blades of populations in eastern Colombia (Vaupés) have a more narrow range of variation, with blades 1.2–4.7× longer than broad and averaging 2.8× longer than the petioles. Populations in the northern extreme of the range in Amazonas in Venezuela have blades ranging from 1.1 to 8.3× (averaging 3×) longer than the petioles, while those in the middle of the range (upper Rio Negro in Brazil) are less variable, with blades ranging from 2.1 to 6.7× (averaging 4×) longer than the petioles. Populations from northwestern Pará in Brazil have proportionately shorter petioles, with blades ranging from 4 to 14× (averaging 7.9×) longer than the petioles.

An unpublished name, *A. disparile* Schott, represented by Schott Drawing 315 (New York Botanical Garden negative #3951 and microfiche 25: C3) based on a collection made by Linden on the Río Orinoco is *A. bonplandii* Bunting subsp. *bonplandii*.

BRAZIL. AMAZONAS: Cachoeira Republica, Rio Curuquete, *Prance et al. 14596* (NY); Camanaus–Uaupes, *Prance et al. 15690* (F, INPA, K, MG, NY, U, US); San Gabriel da Cachoeira, Morro dos Seis Lagos, Lago do Dragão, 400–450 m, *Farney et al. 1714* (MO); Igarapé do Buião, Manaus, *Rodrigues & Chagas 2010* (INPA); Manaus–Caracarai, km 26, *Prance et al. 3073* (INPA, NY, US); Manaus–Porto Velho, trecho Castanho–Tupana, *Silva et al. 200* (INPA); Manaus–São Gabriel, 00°35′S, 64°40′W, *Alencar 252* (NY); 53 km W of Rio Aripuana, Transamazon Hwy., *Calderon et al. 2705* (INPA, MO, US); Santa Isabel do Rio Negro, Campina de Tamendaui, *Madison et al. PFE 39* (INPA), *241* (INPA); 0°23′S, 65°2′W, *Maas 6679* (F, MO); km 795–790 Transamazonica Hwy., Rodovia do Estanho, 7°35′S, 62°30′W, *Vieira et al. 187* (INPA, MG, MO, NY); Pico Rondon, vic. Km 211 of Perimetral N Hwy., 700 m, 1°32′N, 62°48′W, *Pipoly et al. 6658* (MO, NY), *Prance et al. 28768* (INPA, MO, NY), *28785* (MO, INPA, NY); Reserva Biológica do INPA, Manaus, BR-174, Km 45, 500 m, *Anderson 318, 342* (INPA); Mpo. Manaus, Manaus–Caracarai, Campina Preserve, Km 45, less than 100 m, 1°40′S, 60°05′W, *Croat 62207* (INPA, MO); Reserva Florestal Ducke, Manaus, *Ferreira 5877* (INPA); Rio Brancinho, Rio Cuieras, *Prance et al. 17809, 17858* (INPA, NY); Rio Negro, *Maia et al. 689* (INPA); Barcelos–Tapurucuará, *Nascimento 627* (MG, NY); Iauarete, *Coelho & Francisco 203* (INPA); Ilha das Flores, 50 m, *Cavalcante 655* (GM); *Rodrigues 905* (RB), *906* (MO); Manaus–São Gabriel, Morro dos Seis Lagos, 80 km N of São Gabriel, 100 m, 0°20′N, 66°45′W, *Poole 2055* (INPA, MG, MO, NY); Serra de Uaupes, *Rodrigues & Coelho 1466* (MO), *Rodrigues 10718* (NY); Tamendaui, ca. 40 km below Tapurucuará, *Madison et al. 6241* (MO, SEL), *Maia et al. 252* (INPA); Tapurucuará–Mirím, Rio Marie, *Nascimento 656* (MG, MO, NY); *Projecto Flora Epifita 311* (MO); Rio Uaupes, Jutica, *Luetzelburg 23787* (M, R); Taracua, *Cavalcante 747* (GM); Rio dos Pombos, 9 km W of river, ca. 1.5 km E of Igarape dos Pombos, ca. 64 km E of the Aripuanã, 7°10′S, 60°00′W, *Calderon et al. 2606* (INPA); Serra Araca, 0°48′N, 63°18′W, *Pipoly et al. 6782* (NY); Central Massif, 700 m, 0°50′N, 63°17′W, *Prance et al. 29620* (MO, NY); Mpo. Barcelos, Rio Araca, Jauari, afluente de granito, 00°25′N, 63°25′W, *Cordeiro 242* (MO, NY); Mpo. Manaus, Rio Negro, NW of Manaus, *Madison et al. 6311* (K, SEL, US), *6393* (SEL), *Projecto Flora Epifita 39* (INPA). PARA: Cerro de Cupaty, Caqueta, *Lucke 12298* (GM); Rio Jaramacaru, Óbidos, *Egler 282* (MG, RB); Rio

Negro, *Cavalcante 3125* (MG, NY); Mpo. Altamira, Igarapé Ipixuna, affluent of Rio Xingu, 5 km S of settlement, Arawete Indian Reserve, 4°49′S, 52°31′W, *Balee & Ribeiro 1901* (NY); Mpo. Oriximina, Rio Mapuera, 30 km from Cachoeira Porteira, *Cid et al. 1208* (INPA, NY); ca. 10 km upriver from Cachoeira Porteira, *Davidson & Martinelli 10603* (INPA, MG, MO, US, NY); Rio Parú, Cachoeira Chuvisco, *Cid et al. 2228* (INPA, MG, NY); Rio Trombetas, 4 km from margin of Lake Maecue, *Cid et al. 1499* (INPA, NY); 7 km below Cachoeria Porteira, *Cid et al. 1298* (INPA, MG, MO, NY, US); Mpo. Tucuruí, Represa Tucuruí–Breu Branco, BR 422, Km 25, 90 m, 3°52′S, 49°44′W, *Plowman et al. 9564* (MG, MO, NY); Tucuruí, 100–200 m, *Lisboa et al. 2307* (MG). RORAIMA: Manaus–Caracari, Km 515, along bank of Igarapé Dias, *Steward et al. 131* (NY, INPA); Rio Uraricoera, Canal Maraca, Cachoeira Menori, 61°55′W, *Pires et al. 16792* (INPA, MG); Mpo. São Luiz do Anauá, *Ferreira 9233* (MO). COLOMBIA. AMAZONAS: Río Apaporis, Cachivera de Jirijirimo, 250 m, *Schultes 12094* (COL, GH), *Schultes & Cabrera 14083* (GH, NY, U); Río Caquetá, Caño Solarte, *Palacios et al. 1866* (U); Depto. Vichada, Río Mataveni (confluente of Río Orinoco), 100–140 m, *Bunting et al. 3623* (NY). AMAZONAS–VAUPÉS: Río Apaporis, Jirijirimo, 250–300 m, *Garcia-Barriga 13751* (COL, NY, US), *Schultes & Cabrera 12370* (AMES), *12436* (COL, GH), *13466*, *13517* (GH), *13501*, *15952* (AMES), *14641* (AMES, GH), *14051* (GH, U), *14571* (COL, US); Jinogoje, at mouth of Río Piraparana, ca. 350 m, 0°15′S, 70°30′W, *Schultes & Cabrera 17891* (GH). GUAINÍA: Río Negro, junction of Río Negro, Brazo Casiquiare and Río Guainía, 65 m, 2°00′14″N, 67°07′W, *Davidse & Miller 26577* (MBM, MO, VEN); across river from San Fernando de Atabapo (Venezuela), 120 m, 1°47′N, 67°06′W, *Gentry & Stein 46412* (B, K, MO, VEN), *46413* (MO). META: Llanos Orientales, La Macarena, Río Guayabero, Sabanas de Arenisca, 235–700 m, *Garcia-Barriga 17031* (COL, GH, NY, US). VAUPÉS: Cerro de Circasia 300–400 m, *Cuatrecasas 7178* (COL); Río Guainia, Puerto Colombia, opposite Venezuelan town of Maroa, 250–300 m, 2°40′N, 67°30′W, *Schultes & Cabrera 18242* (AMES); Río Kananari, Cerro Isibukuri, 0°15′N, 70°35′W, *Schultes & Cabrera 15082* (GH); affluent of Río Apaporis, *Schultes & Cabrera 13422* (GH); Río Kuduyari, trib. of Río Vaupes, 200–300 m, 1°15′N, 70°05′W, *Schultes & Cabrera 17877* (GH, MO, U); Río Kuduyari, Sabana Yapobada, 350–400 m, *Schultes 22677* (ECON); Río Negro, San Felipe, below confluence of Ríos Guainía and Casiquiare, *Schultes & Lopez 9330* (GH, NY, US); Río Parana–Pichuna, Mitú, *Zarucchi 1348* (COL, MO); Río Piraparana, tributary of Río Apaporis, *Schultes & Cabrera 17475*, *17523* (GH); Río Vaupes, Mitú–Javarete, *Schultes & Cabrera 19266* (AMES); Cerro de Tipiaca, *Schultes & Cabrera 19307* (AMES, GH, U); Circasia, Mitú, *Zarucchi 2047* (COL, K, MO, US). VENEZUELA. AMAZONAS: 200 m, 5°05′N, 65°35′W, *Colchester 2043* (K); Cerro Moriche, Ríos Manapiare and Ventuari, 150–250 m, *Maguire & Maguire 35533* (NY, VEN); Cerro Neblina Region, Cerro Neblina, Río Mawarinuma, 140 m, 0°50′N, 66°10′W, *Croat 59326* (MO, RSA), *59388* (CM, MO), *59627* (B, K, MO, RSA, TEX); Loma de las Piñas (Pineapple Ridge), 1.5 km S of Neblina Base Camp, 150–215 m, 0°49′15″N, 66°9′40″W, *Nee 30554* (MO, NY, VEN); Río Mawarinuma, Cañón Grande, 350 m, 0°50′N, 66°02–06′W, *Davidse & Miller 27132* (VEN), *27174* (MO); 0.5–1.5 km SE of Cerro Neblina, 140 m, 0°50′N, 66°10′W, *Liesner 16147* (MO); Río Baría, 80 m, 1°27′–1°10′N, 66°32′–66°25′W, *Davidse 27683* (VEN); mouth of Río Pasimoni–junction with Río Baría and Río Yatua, 80 m, 1°53–27′N, 66°35–33′W, *Davidse 27780* (MO); Cerro Yapacana, 125–400 m, 3°45′N, 66°45′W, *Steyermark & Bunting 86762*, *103060* (VEN); 825 m, *Steyermark & Bunting 103169* (VEN); Cerros del Casiquiare, 120 m, *Vareschi 6626* (VEN); Río Negro, Piedra de Cocui, *Schultes & López 9423* (GH, US); slope of Cerro Aracamuni, 600 m, *Liesner & Carnevali 22311* (MO); Río Orinoco, Gran Laja near Nericagua, *Morillo 7451* (VEN); 5 km above junction with Caño Cotua, SE of Cerro Yapacana, 100 m, 3°45′N, 66°50′W, *Steyermark & Bunting 102991* (MO, VEN); Cerro Yapacana, 3°45′N, 66°50′W, 140 m, *Sytsma et al. 5103* (WIS); Río Paragua, vic. "Minas de Manaima," 6°7′N, 63°45′W, *Stergios 10289* (MO, PORT); 6°22′N, 66°22′W, *Stergios 10129* (MO, PORT); Caño Cupaven, opposite mouth of Río Atabapo, 125 m, *Wurdack & Adderley 42828* (NY, US, VEN); Sanariapo–point 3 hr upriver by 33 h.p. motor, *Bunting 4255* (MO, MY); Dpt. Casigquiare, Río Temi, Yavita–Pimichín, 5 km from Pimichín, 125–140 m, *Bunting et al. 3774*, *3867* (MY); Yavita–Maroa, 125–140 m, *Bunting et al. 3976* (NY); Río Yatua, base of Cerro Arauicaua, 125 m, 1°35′N, 66°10′W, *Steyermark & Bunting 102532* (MY, VEN), *102543* (VEN); Piedra Arauicaua, 110–550 m, *Maguire et al. 41601* (NY); San Carlos de Río Negro Region, 3–4 km N of San Carlos de Río Negro toward Solano, *Plowman 13536* (MO); Km 11 NE of San Carlos de Río Negro on road to Solano, 75 m, 1°53′N, 67°02′W, *Davidse & Miller 26556* (MO, VEN, W), *26559* (VEN); 115 m, *Berry 1366* (MO, VEN); *Stergios & Aymard 7742* (PORT); near airport, *Croat 59258* (AAU, MO, NY, US), *59260* (B, CAS, F, M, MO, NY); *Steyermark & Bunting 102741* (MO, VEN); 2–6 km NE of San Carlos de Río Negro, 120 m, 1°56′N, 67°03′W, *Liesner 3778*, *6309* (MO), *6137* (VEN), *3277* (MO, SEL), *6402*, *6568*, *6569* (MO, VEN), *Morillo & Hasegawa 5093* (VEN); San Carlos–Solano, 2 km N of San Carlos, 100 m, *Morillo & Villa 5360* (VEN); Dpt. Atabapo, W base of Cerro Yapacana–Caño Cotua headwaters, 100 m, 3°38′N, 66°52′W, *Davidse et al. 17270* (VEN); Caño Caname, Curital de Caname, 100 m, 3°40′N, 67°22′W, *Davidse et al. 16966* (VEN); Dpt. Atures, Isla de Ratón, Carmen, 5°08′N, 67°54′W, *Carnevali et al. 1527* (MO); Río Orinoco, La Esmeralda, *Croizat 208* (NY); Siquita, 100–140 m, *Bunting et al. 3676* (MY); Puerto Ayacucho–Sanariapo, *Bunting 4279* (NY); Sanariapo–San Pedro, *Bunting 4239* (NY), Serranía de Yutaje, 0–1.5 km E of Río Coro–Coro, 4 km N of settlement of Yutaje, 270 m, 5°40′N, 66°7′30″W, *Liesner & Holst 21263* (MO); 3 km W of Río Coro–Coro, 5–8 km NW of settlement of Yutaje, 700–1,000 m, 5°40′N, 66°9′W, *Liesner & Holst 21816* (AAU, B, MO). APURE: Piedra de San Vincente, 80–160 m, *Davidse & Gonzalez 14537* (MO, NY, US, VEN); Dtto. Pedro Camejo, NW of Paso de Cinaruco, 60–65 m, *Davidse & Gonzalez 12467*, *12612* (MO, VEN); Río Meta–Río Cinaruco, Caño El Caballo, 75 m, *Davidse & Gonzalez 15887* (MO, VEN), *13945* (MO, VEN); at jct. of Caño Siriaco, 70 m, *Davidse & Gonzalez 14147* (MO, VEN); Dtto. San Fernando, 60 m, *Davidse & Gonzalez 13895* (F, MO VEN). BOLÍVAR: Mpo. Raul Leoni, 64 km SE of Pijiguaos, 550 m, 06°09′N, 66°23′W, *Delgado 298* (MO).

b. Anthurium bonplandii subsp. **cuatrecasii** Croat, Aroideana 9(1–4): 11–14. 1986. TYPE: Venezuela. Amazonas: Dept. Atabapo, vic. Puerto Ayacucho, along rd. from Puerto Ayacucho to Sanariapo, *Croat 55065* (holotype, MO 2934844; isotypes, B, DUKE, GH, NY, RSA, US, VEN). Figures 56–58.

Terrestrial or epilithic, occasionally epiphytic; stem often caespitose, 1–4 cm diam.; roots dense, mostly descending, the uppermost ascending, grayish when dried, slender and elongate, to 25 cm long, 2–5 mm diam.; cataphylls coriaceous, 4–14 cm long, acute to weakly acuminate at apex, persisting ± intact, eventually dilacerating into fibers at base. *Leaves* erect; petioles 4–30(40) cm long, drying 3–11 mm diam., C-shaped or nearly D-shaped, broadly and sharply sulcate to nearly flattened, with the margins prominently raised adaxially, rounded abaxially; geniculum 0.5–2 cm long; blades coriaceous, oblanceolate, often ± elliptic to slightly ovate-elliptic, rarely oblong-elliptic, acute to weakly acuminate at apex, narrowly rounded to truncate at base, sometimes obtuse, (16)25–55(70) cm long, 4–25(32) cm wide, broadest at or above the middle, the margins weakly undulate; upper surface semiglossy to glossy, medium to dark green above, the lower surface semiglossy, paler, pustulate or glandular-punctate below; midrib scarcely raised at base above, becoming convexly raised toward the middle, prominently convexly raised below; primary lateral veins 5–10 per side, departing midrib at (30)40–55(75)° angle, usually weakly arcuate-ascending to the margin, loop-connecting in the upper ⅓ of the blade, convexly raised; interprimary veins occasionally present; tertiary veins weakly etched above, slightly raised or flat and darker than surface below, prominulous when dried; collective vein arising from near the apex, less prominent than primary lateral veins, often absent, 2–10 mm from margin. *Inflorescences* erect; peduncle (19)30–100 cm long, drying 5–10 mm diam., 1.3–7× as long as petiole, terete; spathe reflexed, usually twisted or recurled, membranous-chartaceous to subcoriaceous, pale yellowish green, sometimes suffused with reddish purple, linear-lanceolate, 5–20 cm long, 0.5–2.5 cm wide, broadest near the base, acuminate at apex (the acumen ca. 5 mm long), decurrent at base; stipe 15–40 mm long; spadix pale green, becoming pink to maroon at maturity, drying green, tapered, erect, (6)10–25 cm long, 5–15 mm diam. near base, 3–6 mm diam. near apex, broadest at the base; flowers rhombic to 4-lobed, drying 1.6–2.6(3.0) mm long, (1.2)1.5–2.6 mm wide, the sides smoothly sigmoid, (4)5–8 flowers visible in either spiral; tepals smooth to somewhat roughened, sometimes whitish muricate; lateral tepals 1.2–1.8 mm wide, the inner margins convex, the outer margins 2–3-sided; pistils ± square, barely or not at all emergent; stigma oblong, ± rectangular, 0.6 mm long, densely papillate; filaments exserted ca. 1 mm; anthers 0.4–1 mm long, 0.4–1.2 mm wide, contiguous, surrounding pistil; thecae drying ± ellipsoid, divaricate. *Infructescence* with spathe withered or absent; spadix (5)10–22 cm long, 0.8–2 cm diam., bearing berries in the basal portion only; berries (immature) green, obovoid, ± truncate at apex, 4–6 mm long, 3–5 mm diam.; pericarp thickened, with raphide cells; seeds 2 per berry, with raphides on the surface, broadly ellipsoid, 4–5 mm long, 1.8–3 mm thick, 1.2–1.4 mm diam., attached to apical end of carpel by strand of fibers.

Anthurium bonplandii subsp. *cuatrecasii* ranges from southern Colombia (Mitú in the Serranía de la Macarena) northeast to the drainage of the middle and upper Río Orinoco in Venezuela (Amazonas) at 75–380 m. Principally found on granite boulders, it often has a caespitose habit, growing in humus tufts either on granite outcrops or terrestrially on soils with a granitic base. It occurs in the tropical dry, tropical moist, and premontane wet forest life zones.

Subspecies *cuatrecasii* differs from the other two subspecies of *A. bonplandii* in having leaves which mostly dry green or greenish and are usually rounded to narrowly truncate at the base, and by its long-pedunculate inflorescence with a usually long-stipitate spadix.

The species is difficult to separate from subsp. *bonplandii* in regions of geographical overlap such as the Mitú area of Vaupés in eastern Colombia or the Middle Orinoco River Basin. *Schultes & Cabrera 19709*, from the Rio Vaupés area near Mitú in Colombia, with both long- and short-stipitate spadices, exemplifies such taxonomic difficulty. It is possible that this collection, and others within this range of sympatry, are the result of local hybridization involving subsp. *bonplandii*.

COLOMBIA. GUIANÍA: Río Orinoco, S of Casuarito, Lejas, 90 m, 5°40′N, 67°37′W, *Davidse & Miller 26370* (MO); across river from San Fernando de Atabapo (Venezuela), 120 m, 1°47′N, 67°06′W, *Gentry & Stein 46412* (B, K, MO, VEN). META: Mun. El Refugio, Parque Nacional Sierra de la Macarena, 10 km E of Refugio, 410 m, *Callejas & Arias 6475* (HUA, MO); Río Guayabero, 10 km below Caño Lozada, 500 m, *Pinto & Jaramillo 208*

(COL); 250 m, *Echerverria 2054* (COL). VAUPÉS: Cerro Mitú, 380 m, *Cuatrecasas 6885* (COL, US), *Schultes et al. 24202* (AMES), *Schultes 22702* (GH); Cerro Mitú–Río Vaupés, 200 m, *Soejarto & Lockwood 2495* (F, K, MEDEL); 350 m, *Maguire et al. 44103* (NY, US); Río Vaupés, Mitú, 250 m, *Schultes & Cabrera 13912* (GH, U); Mitú–Javarete, Arara Cachwira, *Schultes & Cabrera 19397* (GH); Raudal de Yurupari, near Mitú, 0°40′N, 70°30′W, *Schultes & Cabrera 19709* (AMES, GH, MO, NY, U); Mitú, *Zarucchi 1676* (COL, K, MO, US); 350 km above Mitú, Yurupari, 220 m, *Cuatrecasas 6963* (COL, US); Río Inirida, Raudal Guacamayo, 180 m, 69°45′W, *Fernández 2156* (COL, F, US); Río Karuru (tributary of Río Vaupés), Mesa de Yambí, 300–350 m, *Schultes & Cabrera 19147* (AMES), *19194* (AMES, GH, U); Río Kuduyari (tributary of Río Vaupés), Yapoboda, 230–270 m, 1°15′N, 70°05′W, *Schultes & Cabrera 14257* (GH), *14273* (GH, U), *Schultes et al. 18456* (AMES), *Garcia-Barriga et al. 15823A, 15823* (COL, GH). VICHADA: Parque Nacional Natural "El Tuparro," Río Orinoco at mouth at Río Tuparro, 100 m, 5°15′N, 67°51′W, *Zarucchi & Barbosa 3416* (MO). VENEZUELA. AMAZONAS: *Bogner 960* (M); Caño Mosquito, Caño Marieta, *Lister 266* (K); Puerto Ayacucho Region, vic. Puerto Ayacucho, *Huber 612* (M, MO, VEN), *Plowman 7742* (F, K, MO, SEL), *Wessels Boer 1904* (MO, U), *Williams 18379* (VEN); Puerto Ayacucho–Sanariapo, Río Cataniapo, near airport, 100 m, *Croat 55065* (B, MO, NY), *Gentry & Berry 14438* (MO), *Trujillo & Pulido 14958* (MY), *Williams 16037* (F); 3 km N of Puerto Ayacucho, 140–180 m, *Morillo 6753* (MY, VEN); 8 km S of Puerto Ayacucho, Estación de Piscicultura, 85 m, 5°36′N, 67°37′W, *Davidse & Huber 14894* (MO), *Davidse & Miller 26343* (MO); 20 km S of Puerto Ayacucho, N of Caño Garcitas, 100–130 m, 5°33′N, 67°33′W, *Carnevali & Guánchez 1493* (MO); 23 km NE of Puerto Ayacucho, road to El Burro, 80–150 m, 5°51′N, 67°29′W, *Davidse & Huber 15282* (MO, VEN); Isla de El Ratón, 100 m, *Williams 13446* (US, VEN); Río Cataniapo, 80 m from bridge to Sanariapo, 6°25′N, 67°25′W, *Castillo 1237* (MO); Río Guayapo, 10–15 km above mouth of Río Guayapo, tributary to Río Sipapo, 160 m, *Morillo & Ishikawa 3432* (VEN); Río Orinoco, middle and upper parts, *Pannier-Schwabe 1160* (VEN); Santa Rosa–mouth of Río Vichada, Laja Picure, just below Raudal Picure, 100 m, *Maguire et al. 36194* (NY, VEN), *36197* (NY, US, VEN); La Esmeralda, *Medina 349* (VEN); Dpt. Atabapo, Caño Cotua, Yapacana, *Huber 1778* (VEN); Cerro Yureba, Salto Yureba, lower Ventuari, 350 m, 4°03′N, 66°01′W, *Liesner 18654B* (MO); Río Ventuari, 20 km E of Río Orinoco junction, 98 m, 4°03′N, 66°49′W, *Huber 1853* (VEN). BOLÍVAR: mouth of the Paraguaza, Laja del Zamuro, 150 m, *Trujillo 10756* (MY); vic. Minas de Manaima, middle Río Paragua, 6°7′N, 63°45′W, 300 m, *Stergios 10291* (PORT); Río Orinoco, rocky outcrops on Isla Sta. Elena, 100–150 m, *Wurdack & Monachino 39874* (F, NY, US, VEN); Río Paragua, *Badillo 1451* (VEN); Dtto. Cedeño, 35 km SW of Caicara del Orinoco, 100–300 m, 7°30′N, 66°20′W, *Steyermark et al. 131274* (MO).

c. Anthurium bonplandii subsp. **guayanum** (Bunting) Croat, comb. nov. *Anthurium guayanum* Bunting, Acta Bot. Venez. 10: 268. 1975. TYPE: Venezuela. Bolívar: Chimantá Massif, NW part of Abacapa Tepuí, 850–1,100 m, *Steyermark 75100* (holotype, VEN 2005409; isotypes, F, MO, NY). Figures 60–62.

Anthurium corocoroense Bunting, Phytologia 64: 462. 1988. TYPE: Venezuela. Amazonas: Dpt. Atures, Cerro Yutaje, northwest ridge, in montane woodland, 1,500 m, *Maguire & Maguire 35425* (holotype, NY).

Anthurium guaiquinimae Bunting, Phytologia 64: 462. 1988. TYPE: Venezuela. Bolívar: Dtto. Heres, summit of Cerro Guaiquinima, 1–2 km by river above Salto Szczerbani (Río Caparo), 5°44′04″N, 63°41′08″W, 750 m, *Steyermark et al. 113258* (holotype, MO 2581469; isotype, VEN).

Terrestrial or occasionally epiphytic; stem to ca. 20 cm long; internodes short, 1–7 cm diam.; roots dense, spreading, the uppermost ones ascending, thick and blunt at apex, 5–12 cm long, 1–5 mm diam.; cataphylls subcoriaceous or fleshy, 2.5–12 cm long, acute at apex, tinged with red, persisting as coarse linear fibers at base. *Leaves* erect to arching when large; petioles (3)6–30(42) cm long, 8–15 mm diam., C-shaped or sharply D-shaped, sulcate to flattened with the margins sometimes weakly raised and a broad medial rib occasionally present adaxially, rounded abaxially, sometimes 1–2-ribbed; geniculum slightly thicker than petiole, 0.5–1 cm long; blades coriaceous, oblanceolate to obovate, rarely broadly elliptic, acute to obtuse to rounded at apex, long-attenuate to acute or obtuse at base, 30–80(140) cm long, 20–40(65) cm wide, broadest above the middle, the margins undulate; upper surface semiglossy, dark green, lower surface semiglossy to matte, paler and with pustules and glandular-punctations; midrib flat to broadly sulcate at base, sometimes with faint medial rib, becoming prominently convex toward the apex above, higher than broad at base, becoming convexly raised toward apex below; primary lateral veins 6–9(13) per side, departing midib at 40–60° angle, ascending and weakly arcuate to the collective vein, loop-connecting in the upper ⅓, raised in grooves above, raised and paler than surface below; tertiary veins sunken above, raised below; collective vein arising in the upper ⅓ of blade, almost as prominent as primary lateral veins, or often absent, 5–10 mm from margin. *Inflorescences* erect-spreading, nearly as long as or longer than leaves; peduncle 24–96 cm long, 4–10 mm diam., (1.5)4–5(7)× as long as petiole, green tinged with maroon or purple, terete; spathe spreading-reflexed, sometimes inrolled, coiling-recurled or reflexed, subcoriaceous, pale to medium green, sometimes suffused with purple, oblong-lanceolate, (4)8–

18(24) cm long, 1–3.5 cm wide, broadest near the base, acute to shortly acuminate at apex (the acumen ca. 10 mm long), obtusely clasping at base; spadix greenish when young, becoming reddish to purple or purple-brown at anthesis, sessile or subsessile, ± cylindroid, shortly to gradually tapered at apex, erect, 5–33 cm long, ca. 5–7 mm diam. near base, 2–3 mm diam. near apex; flowers (dried) rhombic, (1.6)2.8–3.4 mm long, (1)1.8–2.8 mm wide, the sides straight parallel to spiral, smoothly and weakly sigmoid perpendicular to spiral; 3–7(9) flowers visible in principal spiral, 4–6 in alternate spiral; tepals minutely papillate, sometimes whitish muricate, matte; lateral tepals 1.4–2 mm wide, the outer margins 2-sided, the inner margins broadly convex; pistils squarish, weakly emergent; stigma rectangular, 0.6 mm long, appearing papillate; stamens emerging in a regular sequence from the base, the laterals preceding the alternates by 7–10 spirals, the 3rd stamen preceding the 4th by 6–8 spirals, arranged in a circle, inclined over and obscuring the pistil; anthers yellow, 0.4–0.6 mm long, 0.5–0.8 mm wide; thecae oblong, 0.2–0.3 mm wide, slightly divaricate; pollen white. *Infructescence* with spathe withered, eventually deciduous; spadix 8–35 cm long, to 2 cm diam., bearing berries in the basal portion only, the apical portion sometimes weathering away; berries reddish purple, white in basal ⅓, obovoid, 6–10 mm long, 5–8 mm diam.; pericarp thickened, with raphide cells; seeds 1 or 2 per berry, reddish violet, ellipsoid, weakly flattened, 3–6 mm long, 2–5 mm diam., 1–2 mm thick, attached to carpel wall at radicle end and by a thick strand of fibers.

Anthurium bonplandii subsp. *guayanum* occurs in the Guiana Highlands of Venezuela, Brazil, Guyana, and Surinam, most material being from Bolívar State in Venezuela, at (100)400 to 1,500 m on sandstone outcrops, sandstone boulders or in pure white sand deposits in open areas and in partial shade. It is ecologically variable, occurring in premontane moist, premontane wet, premontane rainforest, and tropical wet forest life zones.

This subspecies is characterized by its usually large, often broad, coriaceous leaf blades which have unusually dark and conspicuous glandular punctations on the lower surface.

It is distinguished from subsp. *bonplandii* mainly by its oblanceolate to obovate (vs. mostly elliptic) leaf shape, and from subsp. *cuatrecasii* by the leaf blades being usually acute at base and drying brown (vs. greenish) and by the sessile to subsessile (vs. usually markedly stipitate) spadix. Both of these subspecies occur at lower elevations than subsp. *guayanum*, usually below 500 m.

The subspecies *guayanum* may be easily confused with the other two subspecies of *A. bonplandii* in areas where their ranges overlap, especially in the upper Río Orinoco drainage and along the rivers of southern Amazonas, Venezuela, that flow into Río Negro.

Two species described recently by Bunting (1988) are synonymized here. Both are compared with only *A. bonplandii*. *Anthurium corocoroense* differs in no way from typical *A. bonplandii* subsp. *guayanum*, and *A. guaiquinimae* differs only in a minor way. Characters which are stressed as important are the broad spathe (to 2.5 cm wide) and the abruptly rounded leaf base. The spathe of subsp. *guayanum* may range to 3.5 cm wide and the abruptly rounded leaf base is an occasional feature on some material of subsp. *guayanum* (see for example *Davidse & Miller 27174* from Cerro Neblina and *Geyskes 16* from Surinam).

BRAZIL. RORAIMA: Serra dos Surucucus, NE of Mission Station, 1,000–1,400 m, 2°42′N, 63°33′W, *Prance et al. 10010* (INPA, NY). GUYANA. MAZARUNI–POTARO REGION: upper Mazaruni River Basin, Karowrieng River, above Maipuri Falls, 550 m, 5°42′N, 60°03′W, *Pipoly & Alfred 7635* (US). SURINAM. Arrowhead basin, Tafelberg, 500 m, *Maguire 24458* (NY, US); Emma Mts., W slope, 600 m, *Boer 1481* (NY); Gonggrijp top, 950 m, *Daniels & Jonker 1286* (U); Gonggrijp top-Hendrik top, Stahel top, 700 m, *Daniels & Jonker 807* (NY). VENEZUELA. AMAZONAS: Dpt. Atures, Río Coro–Coro, W of Serranía de Yutaje, 8 km N of Yutaje, 650–750 m, 5°41′30″N, 66°07′30″W, *Holst & Liesner 3128* (MO); Río Manapiare, Serranía Yutaje, Caño Yutaje, 1,500 m, *Maguire & Maguire 35425* (NY, VEN); Río Orinoco, Esmeralda Ridge, 150–200 m, *Maguire & Wurdack 34642* (NY, VEN); Dpt. Atabapo, Cerro Huachamacari, 1,000 m, 3°39′N, 65°43′W, *Liesner 18228* (MO); Duida–Marahuaca, 1,000–1,200 m, 3°34′N, 65°32′N, *Liesner 25547* (F, DUKE, MO, US); Serranía del Parú (Aroko), 1,100 m, 4°31′N, 65°35′W, *Huber 4345* (VEN); Dpt. Río Negro, Cerro Neblina, N of Puerto Chimo, 500–700 m, 0°50′N, 66°06′W, *Davidse & Miller 27384* (MO); along Río Mawarinuma, Cañón Grande, 300 m, 0°50′N, 66°02–06′W, *Davidse & Miller 27245* (MO). BOLÍVAR: 0–6 km S of El Puaji, 800–900 m, 4°30′N, 61°35′W, *Liesner 19718, 19782* (MO), *Liesner & Holst 18799* (MO); Esmeralda Ridge, Esmeralda, 100 m, *Tate 189* (NY); Santa Elena–Icabarú, 106 km SW of Santa Elena, 13 km NE of Icabarú, Esmeralda, 750 m, 4°19′N, 61°46′W, *Croat 54062* (B, F, GH, MO, US); Canaima, 800 m, *Ferrari 1106* (MY), *Trujillo 6015* (MY), *Bunting 4346* (NY); Quebrada Los Brasileros-road to Playa Blanca and Río Uaiparú, SW of Icabarú, 450 m, 4°20′N, 61°48′W, *Steyermark et al. 117747* (MO, VEN); Cerro Bolívar, Piar, 750 m, *Aristeguieta 2275* (NY); Cerro Guaiquinima, 300 m, *Maguire 32743* (NY, VEN); Salto del Río Szczerbanari (Río Carapo), 1–2 km above Salto Szczerbanari, 750 m, 5°44′N, 63°41′W, *Steyermark &*

Dunsterville 113258 (F, MO, U, VEN), *Steyermark et al. 117258* (MO, VEN); Cerro Marajanu, Alto Caura, 550 m, *Cardona Puig 2959* (MO, VEN); Cerro Sarisarinama, Meseta de Jaua, 700 m, 4°41′N, 64°13′W, *Steyermark et al. 108992* (VEN); Chimantá Massif, Base Camp–slopes above valley of Río Tirica, SW-facing slopes of Chimantá-tepuí (Torono-tepuí), 1,000–1,400 m, *Steyermark 75378* (F, NY, VEN); NW part of Abacapa-tepuí, 850–1,100 m, *Steyermark 75100* (F, MO, NY); Auyán-tepuí, Guayaraca, 1,000 m, *Bogner 1534* (M, MO), *Steyermark 94210* (VEN); Dtto. Piar, Pie de la Roca–Guayaraca, Auyán-tepuí, 600–850 m, 5°43′N, 62°31′W, *Davidse & Huber 22658* (MO); lower part of Río Caroni, Sabana de Arekuna, 6°31′N, 62°53′W, *Prance & Huber 28334* (MO); Río Icabarú and Río Hacha, 450–850 m, *Bernardi 2827* (NY); Río Paragua, Salto de Auraima, 275 m, *Killip 37358* (US, VEN); Sierra Ichun, N of Salto María Espuma (Salto Ichun), near Río Ichun (tributary of Río Paragua), 625–725 m, 4°46′N, 63°18′W, *Steyermark 90240* (BH, US); Dtto. Roscio, 1 km N of Río Samay, 600–800 m, 4°25′N, 61°37′W, *Holst & Liesner 2479* (MO); 7 km NW of Icabarú, 400 m, 4°20′N, 61°51′W, *Steyermark et al. 127301* (B, MO); Mpo. Urucuru, Avequi, "Ciudad Muerte," 500 m, *Bernardi 1687* (NY); Mpo. Urucuru, Río Hueque, Cerro del Papelou, 700 m, *Bernardi 1641* (NY).

Anthurium bradeanum Croat & Grayum, sp. nov. TYPE: Panama. Coclé: Cerro Moreno, Molejón–Coclecito, 13 km NW of Cascajál, 130–250 m, *Davidse & Hamilton 23715* (holotype, MO 3039173; isotypes, B, K, RSA). Figures 63, 64.

Planta epiphytica; cataphyllum lanceolatum, acuminatum, persistens semi-intactum, demum fibris linearibus findens; lamina elliptica ad oblanceolato-elliptica vel ovato-elliptica, (20)25–60 cm longa, 8.5–21 cm lata; nervis primariis lateralis (5)10–15 utroque. Pedunculus 21–58 cm longus, angulatus; spatha ovata, deflexa, cucullata, viridis, 2.5–6(9) cm longa, 2.1–4 cm lata; spadix flavovirens, citreus vel cremeus, clavatus, 1.9–5 cm longus, 8–10 mm diam. Fructus luteus ad albus, ovoideus.

Epiphytic; stem very short, 0.5–1.5 cm diam.; roots moderately dense, descending, green, pubescent, moderately slender and elongate, tapered, 2–4 mm diam.; cataphylls subcoriaceous, lanceolate, 6–9 cm long, acuminate at apex, light green, drying tan (B & K red 9/10), persisting semi-intact, eventually as linear fibers. *Leaves* erect-spreading to spreading; petioles 6–32(40) cm long, 5–7 mm diam., ± quadrangular, occasionally D-shaped, flattened to rounded adaxially, the margins sharply raised but not winged, sharply 2–3-ribbed abaxially (sometimes rounded), the surface pale-speckled; geniculum paler and thicker than petiole, becoming fissured transversely with age, 0.8–2.5 cm long; blades subcoriaceous, elliptic to oblanceolate-elliptic to obovate-elliptic, less than 5× longer than wide, long-acuminate at apex (the acumen apiculate), acute to abruptly attenuate at base, (20)25–60 cm long, 8.5–21 cm wide, broadest at or above the middle, the margins weakly undulate, both surfaces glossy to semiglossy, medium green above, paler below, drying green, semiglossy to matte; midrib flat at base, becoming convexly raised toward the apex, pale-speckled, paler than surface above, sharply 2-ribbed and higher than broad at base, becoming convexly raised toward the apex, paler than surface below; primary lateral veins (5)10–15 per side, departing midrib at 30–40° angle, ± straight to the collective vein or weakly arcuate-ascending, moderately sunken, becoming weakly sunken toward the margin above, prominently and convexly raised below, paler than surface above and below; tertiary veins weakly visible above, slightly darker than surface below; collective vein arising from near the base or about the middle of the blade, sunken above, raised below, less prominent than primary lateral veins, 1–3 mm from margin. *Inflorescences* erect-spreading to spreading, usually shorter than leaves; peduncle 21–58 cm long, equaling or 2–3× longer than petioles, several-angled to subterete with prominent sharp rib abaxially, conspicuously pale-speckled; spathe boat-shaped, about as long as spadix and hooded over it (directed at ca. 180° angle to peduncle), coriaceous, dark green, somewhat discolored along margins, ovate, cucullate, 2.5–6(9) cm long, 2.1–4 cm wide, inserted at 50–70° angle on peduncle, abruptly to gradually acuminate at apex, rounded to truncate at base, decurrent on petiole; spadix deflexed, pale yellow-green to lemon-yellow to creamy-white, (occasionally brownish), sessile, clavate, 1.9–5 cm long, 8–10 mm diam., directed at ca. 90° angle from peduncle; flowers 4-lobed, 1.6–2.2 mm long, 2–2.5 mm wide, the sides jaggedly sigmoid; 16–20 flowers visible in principal spiral, 13–16 in alternate spiral; tepals matte, conspicuously papillate; lateral tepals 0.6–0.9 mm wide, the inner margins straight to convex and turned up against pistil; pistils emergent to 0.5 mm, white to pale greenish white; stigma 0.2 mm long, brush-like, droplets appearing 2–3 days before stamens emerge, persisting for 2 weeks; stamens emerging in a complete sequence, emerging well above tepals then retracting; lateral stamens soon followed by 3rd and 4th stamens, arranged in tight cluster above pistil; filaments whitish, exserted, 0.3–1 mm long, 0.2–0.3 mm wide; anthers pale yellow, 0.3–0.4 mm long, 0.5–0.6 mm wide; thecae ellipsoid; pollen pale yellow fading to white, sweet-scented. *Infructescence* spadix 5–11 cm long; berries greenish yellow to white (also reported as reddish), obovoid, sharply pointed at apex, 4–4.3 mm long, 2.5 mm diam.; seeds 2 per berry, yellowish brown,

oblong-ovoid, flattened, 3.2–3.5 mm long, 1.5–1.9 mm diam., 1.1–1.2 mm thick.

Anthurium bradeanum ranges from Nicaragua to Panama in tropical wet forest life zones from near sea level to usually 450 m, rarely to 800 m.

This species is distinguished by its long, sharply margined petioles, its more or less elliptic leaf blades, its cucullate, coriaceous, ovate spathe, its deflexed, short, clavate, lemon-yellow to white spadix, and yellow to white fruits.

Anthurium bradeanum may be confused with *Anthurium spathiphyllum* where they occur together, such as at the La Selva Biological Station in Costa Rica. Both species have a short clavate spadix, but *A. spathiphyllum* differs in having narrower leaves with 20–30 prominently sunken primary lateral veins (vs. 5–15 scarcely sunken veins in *A. bradeanum*). In addition, *A. spathiphyllum* commonly has three-sided petioles and a lanceolate spathe that is about twice as long as the spadix. In *A. bradeanum*, the spathe is ovate and as long as the spadix.

The species is named in honor of Alexander Curt Brade, who made the first collection of the species in Costa Rica during 1908–1910. The species was not recollected until 1970, when I collected it in Panama at Guásimo in Colón Province.

The species was mistakenly called *A. cuneatissimum* (Engl.) Croat in the revision of *Anthurium* for Central America (Croat, 1983, 1986). That name is now considered synonymous with *A. consobrinum* Schott.

COSTA RICA. ALAJUELA: 15 km WNW of Quesada by air, 1 km W of Jaillos, 150–200 m, 10°23′N, 84°33′W, *Liesner et al. 15175* (MO); 22 km NE of Quesada by air, 4 km W of Muelle San Carlos, 10°28′N, 84°30′W, *Liesner 14112* (CR, K, MO); San Carlos, vic. Florencia, 250 m, *Haber et al. 1854* (MO); between San Miguel and El Pilón, 600 m, 10°43′30″N, 85°00′30″W, *Herrera 2069* (CR, DUKE, MO); Llanuras de San Carlos, *Brade 2539* (BR); Cañas–Upala Road, Río Zapote, 3–4 km NNE of Bijagua 400–450 m, *Burger & Baker 9820* (MO), *Croat 36275, 36296* (MO); 13.8 km N of Bijagua, 100–150 m, *Croat 36454* (B, C, DUKE, F, K, M, MBM, MO, P, QCA, S, U, US); NNE of Bijagua, 200 m, *Croat 36480A* (MO); Río Peje; Ciudad Quesada–Florencia, 1 km E of Florencia, 250 m, 10°21′N, 84°28′W, *Hammel et al. 14032* (MO, US); Monteverde Reserve, Peñas Blancas river valley, 800 m, 10°20′N, 84°40′W, *Haber et al. 5116* (MO). HEREDIA: Puerto Viejo Region, Río Sucio, 20 m, *Croat 35751* (CAS, MO); San José–Puerto Viejo, vic. of Chilamante, 11.6 mi. N of Cariblanco, 10°27′N, 84°05′W, 100 m, *Croat 68361* (MO); Finca La Selva, *Christenson 1532* (MO). LIMÓN: between Barra del Colorado and ocean beach, 0–2 m, 10°47′N, 83°35′W, *Stevens 24092* (MO); 3.5 km S of Islas Buena Vista in the Río Colorado, 16 km SW of Barra del Colorado, 10–120 m, 10°39′N, 83°40′40″W, *Davidse & Herrera 31243* (K, MO); Cerro Coronel, E of Río Zapote, 10–40 m, 10°40′N, 83°40′W, *Stevens et al. 24723* (MO); Reserva Biológica Hitoy Cerere, Río Cerere–Quebrada Barrera, SW of Valle La Estrella, 550 m, 9°39′N, 83°02′W, *Grayum et al. 5810* (MO); 100–250 m, *Gómez et al. 23663* (CR, MO); Río Colorado, 2 km upstream from downstream branch of Caño Bravo, 5 m, 10°43′N, 83°40′W, *Stevens 24018* (MO). NICARAGUA. ZELAYA: 1 km N of Barra de Punta Gorda, 10 m, 11°31′N, 83°46′W, *Moreno 13274* (MO); Río Punta Gorda, Atlanta, landing field, 10 m, 11°34′N, 84°1′W, *Moreno & Sandino 12768* (MO); Atlanta, SE of "La Richard," 30 m, 11°32′N, 84°5′W, *Moreno & Sandino 13117* (MO); Monkey Point, 1.5 km from Caño El Pato, 10 m, 11°35′N, 83°42′W, *Moreno 12373, 12422* (MO); Caño Monte Cristo, Las Faldas, 40–60 m, 11°36′N, 83°51′W, *Moreno 14810* (MO); Río Serrano, 1 km of Colonia Serrano, 70–80 m, 11°34′N, 84°21–22′W, *Sandino 3446* (MO). PANAMA. COCLÉ: Cerro Moreno, Molejón–Coclecito, 13 km NW of Cascajal, 130–250 m, 8°46′44″N, 80°31′54″W, *Davidse & Hamilton 23715* (B, K, MO, RSA); El Copé Region, N of El Copé, Limón, *Folsom 5815* (MO, PMA). COLÓN: Río Miguel, Guásimo, *Croat 9902* (MO, PMA, SEL).

Anthurium brenesii Croat & R. A. Baker, Brenesia 16(Suppl. 1): 28. 1979. TYPE: Costa Rica. Alajuela: along Hwy. 15 between Naranjo and Quesada, 3.2 mi. N of Zapote, 1,560 m, *Croat 46923* (holotype, MO 2682420; isotypes, COL, CR, DUKE, F, GH, K, MEXU, NY, P, PMA, RSA, SEL, U, US, VEN). Figures 65, 67–69.

Epiphytic; stem usually pendent, less than 30 cm long, 1.5–2.5 cm diam.; roots sparse, descending, green to brown, pubescent, thick, elongate, slightly tapered, 5–7 mm diam.; cataphylls moderately coriaceous, weakly ribbed near apex, 10–25 cm long, acuminate at apex, drying light brown, persisting semi-intact, eventually as a reticulum of fibers. *Leaves* spreading to pendent; petioles 11.5–45 cm long, 3–6 mm diam., terete, rounded to obtusely and obscurely sulcate adaxially, the surface pale-speckled; geniculum somewhat thicker than petiole, 1.5 cm long; blades coriaceous, oblong-elliptic to oblong, acuminate at apex (the acumen minutely inrolled), acute to obtuse to narrowly rounded at base, 16–68 cm long, 4.3–10.3 cm wide, broadest at or near the middle, the margins weakly undulate; both surfaces matte to weakly glossy, dark green above, paler below, drying yellowish green; midrib bluntly angular-raised above, pale-spotted in lower half, prominently convexly raised, much paler than surface below; primary lateral veins 13–16 per side, scarcely more conspicuous than interprimary veins, departing midrib at 35–45° angle, broadly arcuate, weakly sunken above, weakly raised and darker than surface be-

low; tertiary veins obscure above and below; collective vein arising from the base, slightly sunken above, raised and darker than surface below, equally as prominent as primary lateral veins, 2–5 mm from margin. *Inflorescences* shorter than leaves; peduncle (10)28–43 cm long, 4–5 mm diam., 2–3/4× as long as petiole, terete; spathe erect and somewhat hooded over the spadix, moderately coriaceous, medium green, sometimes tinged with red or violet-purple, ovate to ovate-elliptic, 5.5–8.5 cm long, 3.5–5.5 cm wide, broadest just above the base or near the middle, inserted at 25–40° angle on peduncle, acute to rounded at apex (the acumen apiculate), cordate and somewhat clasping at base; spadix green to red-brown to red-violet to purple, short-cylindroid, somewhat stubby, 3.2–8 cm long, 6–8 mm diam.; flowers ± square to weakly 4-lobed, 1.7–2.5 mm in both directions, 6–10 flowers visible in either spiral; lateral tepals 0.8–1.2 mm wide, the inner margins straight to broadly convex, the outer margins 2–3-sided; pistils scarcely emergent; stigma oblong, 0.5–0.6 mm long; stamens held just above tepals; filaments short, translucent, soon retracting to hold anthers at level of the tepals; anthers orange, (0.4)0.6 mm long, (0.5)0.8 mm wide; thecae ovoid-ellipsoid, slightly divaricate; pollen orange, faintly spicy-scented. *Infructescence* spreading to pendent; spathe usually dried; spadix to 9 cm long, 2 cm diam.; berries orange (B & K yellow-red 7/5), obovoid, rounded at apex, 9–11 mm long, 5–7.5 mm diam.; pericarp thin, lacking raphide cells; mesocarp juicy, with sparse, thick sclereids; seeds 2 (rarely 1) per berry, light brown, 3–4.5 mm long, 2.2–3 mm diam., 1.8–2.2 mm thick, enveloped by an almost translucent envelope extending to 10 mm long and as wide as seed.

Anthurium brenesii is known from 800 to 1,560 m on the Atlantic slope in the Cordillera Volcánica and the Cordillera Central in the provinces of Alajuela and Guanacaste in a premontane rainforest life zone.

This species is distinguished by its oblong to oblong-elliptic leaf blades with rather obscure primary lateral veins and the collective vein arising from the base, and by its broad spathe, cylindroid spadix, and orange berries.

Anthurium brenesii is related to *A. protensum*, with which it shares similar leaf texture and cataphylls and a similar altitudinal range. It differs from that species by its abruptly acuminate leaf blades, its short, broad spathe which is subcordate at the base, and its shorter, broader spadix. It is also similar to *A. prolatum*, but differs in having much shorter, broader leaves and a shorter, stubbier spadix and an erect, more or less ovate spathe. In contrast, *A. prolatum* has a spadix many times longer than broad (more than 50×) and a linear-lanceolate spathe.

COSTA RICA. ALAJUELA: between Naranjo and Quesada, 3.2 mi. N of Zapote on Hwy. 15, *Croat 46923* (COL, CR, DUKE, F, GH, K, MO, NY, P, PMA, RSA, SEL, U, US, VEN); La Palma de San Ramón, *Brenes 5738* (F); Reserva de San Ramón, 800–1,000 m, 10°12′53″N, 84°36′28″W, *Herrera & Mora 180* (CR, MO), *Herrera et al. 411* (B, CR, MO); Cordillera Central, ca. 15 km N of Zarcero, *Williams et al. 29034* (F). GUANACASTE: Santa Elena–Laguna de Arenal, 4 km N of El Dos de Tilarán, 1,000 m, 10°23′N, 84°53′W, *Hammel et al. 15134* (MO), *Haber & Bello 6549* (MO); Parque Nacional Rincón de la Vieja, SE slopes of Volcán Santa María, above Estación Santa María, 900–1,200 m, 10°47′N, 85°18′W, *Davidse et al. 23448* (CR, K, MO); 1,000 m, *Baker R20* (BM); 900–1,000 m, *Herrera 1609* (MO); 1,100–1,300 m, *Herrera 1405* (MO).

Anthurium bucayanum Croat, sp. nov. TYPE: Ecuador. Guayas: Río Chimbo, 0.9 km E of junction to El Triunfo at edge of General Elizalde (Bucay), 2°12′S, 79°05′W, 510 m, *Croat 61597* (holotype, MO 3422020-24; isotypes, AAU, B, BM, CAS, CM, GH, K, NY, QCA, RSA, SEL, US). Figures 66, 70–72.

Planta epiphytica aut terrestris; internodia brevia, 1.5–4 cm diam.; cataphyllum lanceolatum, persistens semi-intactum; petiolus (5.5)9–14 cm longus, 4–10 mm diam., acute D- aut C-formatus; lamina late oblanceolato-elliptica ad oblanceolatae, (38)50–112 cm longa, (10)15–26.5 cm lata; nervis primariis lateralis (13)18–26 utroque. Pedunculus 34–48 cm longus, ca. 4 mm diam.; spatha oblongo-elliptica, 13.5–15 cm longa, 3 cm lata; spadix cylindricus infirme contractus, 8.5–10 cm longus, 6–8 mm diam. prope basim, 4–5 mm diam. prope apicem, atropurpureus. Baccae 4.5–6 mm longae, 3–3.2 mm latae.

Epiphytic or terrestrial; stem to ca. 60 cm long, 1.5–4 cm diam.; roots dense, ascending, pale greenish, conspicuously pubescent, short to moderately elongate, bluntly pointed at apex, 2–5 mm diam.; cataphylls membranous, lanceolate, unribbed, 2.5–12 cm long, acute at apex with a subapical apiculum, green, drying light brown with dense raphides, persisting semi-intact, eventually deciduous. *Leaves* erect to spreading; petioles (5.5)9–14 cm long, 4–10 mm diam., acutely D-shaped to C-shaped, broadly convex adaxially with the margins sharply raised and slightly turned inward, 5–10-ribbed abaxially, the surface somewhat pale-speckled; geniculum slightly thicker and paler than petiole, fissured transversely with age, 1–2 cm long; blades subcoriaceous (very thin on drying), broadly oblanceolate-elliptic to oblanceolate, acute to shortly acuminate at apex (the acu-

men weakly inrolled), narrowly acute to acute to narrowly rounded at base, (38)50–112 cm long, (10)15–26.5 cm wide, broadest at or above the middle, the margins broadly and shallowly undulate; upper surface glossy to semiglossy, medium green (B & K yellow-green 4/10), lower surface semiglossy; both surfaces drying semiglossy to weakly glossy, dark green to yellow-green; midrib broadly convex to obtusely flat-raised and obscurely sulcate above, higher than broad and bluntly 3–5-ribbed at base, becoming prominently convexly raised toward the apex below; primary lateral veins (13)18–26 per side, departing midrib at 55–75° angle, straight (sometimes weakly arcuate) to the collective vein, prominently convex above and below; tertiary veins weakly visible when fresh below, prominulous when dried; collective vein arising from near the base, weakly sunken above, weakly raised below, drying weakly raised above and below, less prominent than primary lateral veins, 3–10 mm from margin. *Inflorescences* erect to erect-spreading; peduncle 34–48 cm long, ca. 4 mm diam., 3.3–4.2× as long as petiole, drying blackish brown, terete; spathe spreading-recurled, subcoriaceous, green, oblong-elliptic, 13.5–15 cm long, 3 cm wide, acute at apex; stipe 5.5–7 cm long in front, 5.3–6 cm long in back; spadix dark violet-purple, blackish when dried, weakly tapered, ± erect, curved, 8.5–10 cm long, 6–8 mm diam. near base, 4–5 mm diam. near apex; flowers square to rhombic, 1.5–2 mm long, 1.2–1.9 mm wide, the sides ± straight; (5)6–9 flowers visible in principal spiral, (8)9–12 in alternate spiral; tepals matte; lateral tepals 1.3–1.5 mm wide, the inner margins straight to concave, the outer margins 2-sided; pistils weakly exserted; stigma slitlike, ca. 0.3–0.4 mm long; anthers ca. 0.4–0.5 mm long, (0.4)0.5–0.6 mm wide; thecae oblong, not divaricate. *Infructescence* with spathe withered; spadix 17.5 cm long, ca. 1.2 cm diam.; berries (rehydrated) oblong, apparently rounded at apex, ca. 4.6–5 mm long, 3–3.2 mm diam.; seeds 2 per berry, yellow-brown with darker punctations, oblong-ovoid to somewhat broadly ellipsoid, slightly flattened laterally, 2.9–3.5 mm long, 2–2.3 mm diam., 0.9–1.5 mm thick.

Anthurium bucayanum is endemic to Ecuador, in the provinces of Guayas and Cotopaxi at 510–690 m in lower montane wet forest and premontane moist forest life zones.

This species is characterized by its epiphytic habit, its large very thin-drying, broadly oblong-oblanceolate to elliptic leaf blades which dry mostly dark green and have a collective vein arising from the base and running close to the margin, and by its prominently stipitate, curved spadix.

Anthurium bucayanum is similar in appearance to *A. campii*, with which it shares general blade shape and size and overall spadix appearance. *Anthurium campii* differs in having much more coriaceous leaf blades and a sessile, green spadix, and occurring at higher elevations (1,200–2,000 m vs. 510–690 m). *Anthurium bucayanum* also resembles *A. sparreorum* (also from lowland coastal Ecuador) in overall appearance, but the latter differs in having thicker leaf blades, a subsessile spadix and perianth which becomes fleshy and conspicuous in fruit.

The species is named for the town of Bucay, near which it was first collected.

ECUADOR. COTOPAXI: 2 km N of Pucuyacu near bridge over Río San Francisco, 690 m, 0°41′S, 79°06′W, *Croat 57082* (MO). GUAYAS: Río Chimbo, Bucay–Río Bamba, Bucay, 510 m, 2°15′S, 79°5′W, *Croat 50912* (MO); 900 m E of junction to El Triunfo at edge of General Elizalde (Bucay), Los Ríos, border of Bolívar and Chimborazo provinces, 510 m, 2°12′S, 79°5′W, *Croat 61597* (AAU, B, BM, CAS, CM, GH, K, MO, NY, QCA, RSA, SEL, US).

Anthurium bushii Croat, sp. nov. TYPE: Ecuador. Morona–Santiago: Cordillera de Cutucú, along trail from Logrono to Yaupi, *Madison et al. 3285* (holotype, SEL 014964). Figure 73.

Planta epiphytica; internodia et cataphylla ignota; petiolus 8 cm longus, 7 mm diam., D-formatus; lamina oblanceolata, ca. 100 cm longa, 18.5 cm lata; nervis primariis lateralis ca. 21 utroque. Pedunculus 36 cm longus, ca. 2 mm diam.; spatha verisimiliter lanceolata, 8 cm longa, ca. 1.3 cm lata, purpurea; spadix oblongo-cylindricus, 12 cm longus, medio ca. 4 mm diam., colore ignoto. Baccae ignotae.

Description based on dried material only. Epiphytic; stem and cataphylls unknown; petioles 8 cm long, 7 mm diam., D-shaped, with medial rib and the margins sharply raised adaxially, probably rounded abaxially; geniculum conspicuously thicker and somewhat darker than petiole, 0.7 cm long; blades subcoriaceous, oblanceolate, narrowly acute at apex, very long-attenuate at base, ca. 100 cm long, 18.5 cm wide, broadest above the middle, the margins moderately undulate; both surfaces matte, grayish green, slighty paler below; midrib ± acutely raised above, slightly paler than surface, broadly convexly raised and brownish below; primary lateral veins ca. 21 per side, departing midrib at 40–50° angle, usually straight, sometimes weakly arcuate to the margin, conspicuously raised above and below, the same color as the midrib; tertiary

veins weakly visible, flat to weakly raised above and below; collective vein absent. *Inflorescences* erect; peduncle 36 cm long, ca. 2 mm diam., 4.5× as long as petiole, drying the same color as midrib, terete; spathe spreading-ascending, subcoriaceous, purple, drying brown, lanceolate, 8 cm long, ca. 1.3 cm wide, acuminate at apex (the acumen inrolled, 13 mm long), narrowly acute at base; spadix drying brownish, oblong-cylindroid, slightly curved, 12 cm long, ca. 4 mm diam. midway; flowers square to rhombic, ca. 4–7 flowers visible in principal spiral tepals ± smooth; lateral tepals 4 mm wide, the inner margins broadly convex, the outer margins 2-sided; anthers 0.4–0.5 mm long, 0.6 mm wide; thecae slightly divaricate. *Infructescence* not seen.

Anthurium bushii is known only from the type collection from the Province of Morona–Santiago in Ecuador, where it was collected in the Serranía de Cutucú at 1,300 m in a premontane moist forest life zone.

This species is characterized by its very long, oblong-oblanceolate blades which dry grayish green and are very long-tapered in the lower third, and by its purplish spathe and slender, cylindroid spadix which dries brown.

This species is probably most closely related to *A. harlingianum*, which differs in having proportionately broader leaf blades, which are mostly truncate to shallowly cordate at the base and usually dry brown.

The species is named in honor of E. O. (Mike) Bush III, former superintendent of Selby Gardens, who accompanied Michael Madison when the type collection was made. He is now at Bermuda Botanical Gardens.

ECUADOR. MORONA–SANTIAGO: Cordillera de Cutucú, W slopes, Logroño–Yaupi, 1,300 m, 2°46′S, 78°6′W, *Madison et al. 3285* (SEL).

Anthurium campii Croat, sp. nov. TYPE: Ecuador. Chimborazo: along road between Alausi and El Triunfo, 6.9 km W of Huigra, 2°19′S, 79°0′W, 1,350 m, *Croat 61562* (holotype, MO 3420768-71; isotypes, B, CM, K, NY, QCA, RSA, US). Figures 74–76, 79, 80.

Planta terrestris aut epiphytica; cataphyllum 22–40 cm longum, lanceolatum, persistens intactum vel semiintactum; petiolus (3)17–23 cm longus, (6)10–15 mm diam., D-formatus, trapeziformis vel C-formatus; lamina late oblanceolata vel oblonga-elliptica, (46)90–145 cm longa, 23–37 cm lata; nervis primariis lateralis 14–40 utroque; nervis collectivis de basi exorientibus. Pedunculus (36)50–85 cm longus; spatha oblonga-lanceolata, (7)13–20 cm longa, 1.3–2 cm lata; spadix 12–23 cm longa, 5–9 mm diam., viridis. Baccae purpureae.

Terrestrial or epiphytic; stem short, 3.5–5.5 cm diam.; roots dense, upper ones ascending, lower ones descending, whitish to grayish, woolly-pubescent, moderately tapered, ca. 3–12 cm long, 4–5 mm diam.; cataphylls thickly coriaceous, lanceolate, 22–40 cm long, obtuse at apex, medium green, drying medium brown, persisting intact or semi-intact, eventually as coarse linear fibers. *Leaves* erect-spreading; petioles (3)17–23 cm long, (6)10–15 mm diam., thicker than broad to D-shaped to trapezoidal or C-shaped, sharply to broadly V-sulcate adaxially with the margins raised, sharply 2–9-ribbed abaxially; geniculum conspicuously thicker than petiole, 1–2.5 cm long; sheath 9–13 cm long; blades coriaceous to subcoriaceous, broadly oblanceolate to oblong-elliptic, rounded to obtuse or sometimes acute at apex, acute at base, (46)90–145 cm long, 23–37 cm wide, broadest above the middle, the margins slightly undulate; upper surface matte to semiglossy, dark green, lower surface semiglossy to glossy, paler; midrib broadly convex at base, becoming flat-raised toward the middle and narrowly convex at the apex above, trapezoidal and 3-ribbed at base, becoming acutely angled and then convex toward the apex below; primary lateral veins 14–40 per side, departing midrib at 50–70° angle, straight or slightly arcuate to the collective vein, convexly raised above, less conspicuously so below; interprimary veins sometimes present, inconspicuous to almost as conspicuous as primary lateral veins; tertiary veins darker than surface and flat below, moderately indistinct; reticulate veins prominulous above and below (or not visible) on drying; collective vein arising from or near the base, equally as prominent as primary lateral veins, 1–13 mm from margin. *Inflorescences* erect; peduncle (36)50–85 cm long, (3)5–6 mm diam., 2.5–3(6)× as long as petiole, terete to bluntly or sharply multiribbed; spathe spreading, with the margins curled under, subcoriaceous, medium green, becoming yellowish, oblong-lanceolate, (7)13–20 cm long, 1.3–2 cm wide, broadest near the base, inserted at 30° angle on peduncle, shortly acuminate at apex, acute at base; spadix medium green, sessile or shortly stipitate, cylindroid to long-tapered, erect to curved, (8)12–23 cm long, 5–9 mm diam. near base, 3–4 mm diam. near apex; flowers rhombic, 1.7–2.6 mm long, 1.1–1.9 mm wide, the sides straight to smoothly sigmoid; 6–13 flowers visible in principal spiral, 5–7 in alternate spiral; tepals matte; lateral tepals 1–1.3 mm wide, the inner margins rounded, erose, the outer mar-

gins 2-sided; pistils weakly emergent; stigma ellipsoid to broadly ellipsoid; anthers tan, 0.5–0.6 mm long, 0.6–0.7 mm wide; thecae oblong, not divaricate; pollen yellow fading to white. *Infructescence* (immature): spreading(?); spathe reflexed and persistent, green; spadix 22–30 cm long, 1.4 cm diam.; berries light purple; pericarp with raphide cells; seeds unknown.

Anthurium campii is endemic to Ecuador in southern Bolívar and southwestern Chimborazo provinces at 1,200 to 2,150 m as an epiphyte or terrestrially in either lower montane dry or premontane dry forest life zones (life zone uncertain).

This species is distinguished by its very large, broadly oblanceolate to oblong-elliptic, coriaceous leaf blades which dry green or yellowish green, its very long, thick cataphylls, and by the collective vein which arises from the lowermost portion of the blade. Its closest ally, and the only species with which it might be confused, is *A. sparreorum*, which occurs at 210–250 m in Cotopaxi and Los Ríos provinces and has shorter cataphylls (9–18 cm vs. 22–40 cm long), a much shorter, stubby, reddish violet spadix on a short peduncle, and a perianth becoming fleshy in fruit and extending beyond the red berry. *Anthurium campii* is also similar in overall appearance to *A. bucayanum*, which has very thin leaves and a long-stipitate, dark violet-purple spadix.

Anthurium campii is named in honor of Wendell H. Camp, who collected during 1944 and 1945 in Ecuador under the auspices of the New York Botanical Garden, and who was one of the first collectors of the species.

Occasional herbarium specimens of a different species have been seen bearing the name "*campii*," as proposed by A. D. Hawkes but never published. These specimens are attributable to *A. andicola* Liebm., an unrelated species of sect. *Belolonchium* from Mexico, and are not to be confused with this new Ecuadorian species.

ECUADOR. BOLÍVAR: Valle de Tablas, 1,200 m, *Acosta Solís 6075* (MO, F). CHIMBORAZO: Alausí–El Triunfo, 6.9 km W of Huigra, 1,350 m, 2°19′S, 79°0′W, *Croat 61562* (B, CM, K, MO, NY, QCA, RSA, US); Río Chanchán, 5 km N of Huigra, 1,650–2,150 m, *Camp 3428* (MO), *E-3360, E-3460* (NY).

Anthurium carchiense Croat, sp. nov. TYPE: Ecuador. Carchí: vic. Maldonado, 1,500–1,900 m, *Madison 3998* (holotype SEL-027098; isotype, MO-2925092). Figures 77, 78, 81.

Planta terrestris aut epiphytica; internodia 6–8 cm longa, 0.8–2 cm diam.; cataphyllum anguste lanceolatum, persistens fibris subtilibus et reticulatis; petiolus teres vel D-formatus 7–17(30.5) cm longus, 4–5 mm diam.; lamina oblonga aut oblanceolata, 30–57 cm longa, 2.7–6 cm diam.; nervis primariis lateralis 13–16 utroque; nervis collectivis de basi exorientibus. Pedunculus 17.5–39 cm longus; spatha 3–6.5 cm longa, 6–10 mm lata; spadix cylindricus, purpureus ad porphyreus, 2.3–6.3 cm longus, 3–5 mm diam.; stamina exserta. Baccae aurantiaco-rubrae, 6–7 mm longae, 3.2–3.4 mm diam.

Terrestrial or epiphytic; stem ca. 6–8 cm long, 0.8–2 cm diam.; leaf scars obscured by cataphyll fibers, 5–6 mm high, 1–1.3 cm wide; roots moderately numerous, generally descending, pale grayish white, drying tan, smooth, short to elongate, blunt at apex, to 14 cm long, 1–4 mm diam.; cataphylls subcoriaceous, narrowly lanceolate, unribbed, 5–9 cm long, acuminate at apex, green, drying tan to dark brown, persisting as a reticulum of fibers. *Leaves* spreading; petioles 7–17(30.5) cm long (mostly less than 16 cm long), 4–5 mm diam., terete to D-shaped, rounded to bluntly and narrowly sulcate (rarely broadly and sharply sulcate) adaxially, rounded abaxially, the surface somewhat pale-speckled; geniculum slightly paler and thicker than petiole, 0.7–2 cm long; blades subcoriaceous to coriaceous, oblong to oblong-elliptic, sometimes somewhat lanceolate or oblanceolate, long-acuminate (rarely acute) at apex, narrowly acute at base, 30–57 cm long, 2.7–6 cm wide, broadest at or slightly above the middle, the margins flat; upper surface glossy to semiglossy, dark green above, matte when dried, lower surface glossy, paler below, semiglossy when dried; both surfaces greenish to yellowish on drying; midrib acutely raised above, prominently and sharply acute below, slightly paler than surface; primary lateral veins 13–16 per side, departing midrib at 50–60° angle, ± straight-ascending to the collective vein, flat above, obscure and very weakly raised below; interprimary veins numerous, obscure above and below, drying raised and almost as conspicuous as primary lateral veins; tertiary veins visible when dried; collective vein arising from or near the base, weakly sunken above, raised below, raised above and below when dried, 3–8 mm from margin. *Inflorescences* erect to spreading; peduncle 17.5–39 cm long, drying 1–4 mm diam., 1.9–5.5× as long as petiole, green (brown when dried); spathe reflexed, subcoriaceous, pale green tinged with purple at margins, oblong-lanceolate to lanceolate, 3–6.5 cm long, 0.6–1 cm wide, broadest near the base, inserted at 45° angle on peduncle, acuminate at apex, acute at base, the margins meeting at 60–

80° angle; stipe 2–6 mm long; spadix maroon to orange-brown to brownish purple to brown (B & K yellow 4/5), cylindroid, shortly stipitate, straight or sometimes curved, 2.3–6.3 cm long, 3–5 mm diam.; flowers ± rhombic, 2–2.4 mm long, 1.5–2 mm wide, the sides straight to smoothly sigmoid on drying; 4–6 flowers visible in principal spiral, 7–9 in alternate spiral; tepals purple-red, papillate, matte; lateral tepals 0.8–1.5 mm wide, the inner margins convex, the outer margins 2-sided; pistils scarcely emergent at anthesis, raised, purple-red to dark purple; stigma slitlike, 0.5–0.6 mm long, forming droplets before stamens emerge; stamens emerging in a regular sequence, held well above tepals, the laterals followed by alternates in rapid succession, the laterals preceding the alternates by 3–4 spirals, arranged in a circle around the pistil; filaments translucent, exserted 0.7–0.8 mm, 0.2 mm wide; anthers orange to pink (B & K red 8/10), 0.2–0.3 mm long, 0.4 mm wide; thecae ovoid, 0.6–0.4 mm wide, slightly divaricate; pollen white. *Infructescence* with spathe persisting; spadix 3.5–10.5 cm long, 1–1.7 cm diam., with the berries scattered throughout; berries orange-red, ± ellipsoid to ovoid, acute at apex, (dried) 6–7 mm long, 3.2–3.4 mm diam.

A member of series *Multinervia*, *Anthurium carchiense* occurs in Ecuador in the Province of Carchí (hence the name), and in Colombia in Nariño at 1,200–2,600 m in premontane wet, premontane dry, and premontane thorn forest life zones; it presumably occurs also in premontane moist forest as well.

This species is distinguished by its small size, more or less oblong leaf blades which are long-acuminate at the apex, maroon to brownish spadix, flowers with exserted stamens, and red-orange berries.

A species similar in overall appearance, *A. obscurinervium*, differs in having a green spadix and D-shaped petioles, and generally occurs at lower elevations.

COLOMBIA. NARIÑO: Cerro Gualcala, W slopes, vic. of Tuquerres, 2,400–2,600 m, *Lehmann 5331* (F, K); La Planada, 7 km above Chucunes on road Tuquerres–Ricaurte, 1,780 m, *Croat 69571* (B, COL, K, M, MO, PSO); near Ricaurte, 1,800 m, *Gentry et al. 59681* (MO). ECUADOR. CARCHÍ: Río San Juan, Chical, 12 km below Maldonado, 1,200 m, 1°4′N, 78°17′W, *Madison et al. 4762* (K, SEL), *4812* (SEL); Chical, 1,200–1,250 m, 0°56′N, 78°11′W, *Thompson & Rawlins 995* (CM); Gualpi Chico area near Awá Ethnic encampment, 1,300 m, 0°58′N, 78°16′W, *Hoover et al. 2752, 3212* (MO); Quebrada Peñas Blancas–Quebrada Quinchul, 0°58′N, 78°12′W, *Thompson & Rawlins 1031* (CM); Maldonado, 1,500–1,900 m, *Madison 3998* (MO, SEL), *4264* (SEL); Río Chilma, Machinas–Planada de Chilma, 2,350–2,450 m, 0°52′N, 78°3′W, *Stein 2913* (MO); Río Verde, Rafael Quindís mountain finca, 1,890 m, 0°52′N, 78°08′W, *Hoover 1986, 2265* (MO); 1,870–2,400 m, 0°52′N, 78°07′W, *Hoover 2265* (MO).

Anthurium cataniapoense Croat, Aroideana 9(1–4): 18–20. 1986. TYPE: Venezuela. Amazonas: Dept. Río Negro, vic. Cerro Neblina base camp, Río Mawarinuma, 140 m, 00°50′N, 66°10′W, *Croat 59319* (holotype, MO 3401082-3; isotypes, AAU, B, CAS, COL, F, INPA, K, M, MY, US, VEN). Figures 82–85.

Epiphytic; stem 1.5–2.5 cm diam.; roots dense, spreading–ascending, ca. 3–12 cm long, ca. 3–4 mm diam.; cataphylls hook-shaped, to 6 cm long, acute and shortly apiculate at apex, drying dark brown to reddish brown, persisting as linear fibers. *Leaves* erect-spreading; petioles 6–13 cm long, 11–14 mm diam., D-shaped, flattened when young, broadly sulcate and with a prominent medial rib adaxially, 1–3-ribbed or rounded abaxially; geniculum paler and thicker than petiole, 1–1.5 cm long; sheath to 5 cm long; blades subcoriaceous, broadly elliptic-oblanceolate, acute to obtuse at apex (the acumen inrolled), narrowly acute to rounded at base, 60–117 cm long, 20–50 cm wide, broadest above the middle, the margins broadly undulate; both surfaces semiglossy, green (B & K yellow-green 6/5); midrib acutely raised, becoming higher than broad toward the apex above, concolorous with the surface, acutely raised and paler than surface below; primary lateral veins 11–16 per side, departing midrib at 40–60° angle, arcuate-ascending to the margin, weakly rounded-raised and concolorous with the surface above, obscurely raised and paler than surface below; tertiary veins flat and darker than surface below; collective vein arising from near the apex or absent, less prominent than primary lateral veins, 5–13 mm from margin. *Inflorescences* pendent; peduncle 32–53 cm long, 3–4 mm diam., (3)5–6(8)× as long as petiole; spathe spreading, subcoriaceous, green, sometimes tinged brownish or purplish adaxially, lanceolate-oblong, 9–26 cm long, 1–2.5 cm wide, acuminate at apex, acute at base; spadix maroon to dark purplish violet (B & K red-purple 2/2.5), sessile, tapered-cylindroid, slightly curved, 11.5–24.5 cm long, 3–5 mm (6.5) diam. at anthesis midway, 3 mm diam. near apex; flowers rhombic, 1.5–2.3 mm long, 1–1.6 mm wide; the sides sigmoid; 8–12 flowers visible in principal spiral, 6–13 in alternate spiral; tepals matte, smooth; lateral tepals 0.5–1 mm wide, the outer margins

2-sided, the inner margins straight to rounded; stigma linear-elliptic, 0.4–0.5 mm long; anthers 0.6–0.8 mm long, 0.6–0.8 mm wide; thecae oblong-obovoid, slightly divaricate. Fruits purple (observed by Anibal Castillo, Puerto Ayacucho).

Anthurium cataniapoense is endemic to the northern Amazon basin in Venezuela, in the basin of the Río Negro and the Río Orinoco in Amazonas and Bolívar at less than 300 m. A specimen from northern Pará in Brazil, in the Tumucumaque Mountains, also appears to belong here. The plants are epiphytic in the understory of mature, well-shaded forest, occurring on white sand soils in a tropical moist forest life zone.

This species is characterized by its broadly oblanceolate-elliptic, short-petiolate leaves which dry greenish brown to brown below and grayish brown to almost black above and have one to three pairs of primary lateral veins arising within the lower 1 cm of the base of the blade. Further characterizing the species is the slender, long-pedunculate, pendent inflorescence and the obtusely D-shaped petioles which are obtusely 1-ribbed adaxially and 1–3-ribbed or rounded abaxially.

This species is closest to *A. loretense* from the western Amazon basin in northeastern Peru, with which it shares similar leaves, hook-shaped cataphylls, and a pendent inflorescence. That species differs, however, in having a much stouter spadix and a longer, stouter peduncle.

An aberrant specimen from Bolívar (*Delascio & López 2812*) is tentatively placed here. It differs in having relatively small leaves (ca. 44 cm × 11–12 cm vs. 60–117 cm × 20–50 cm) and a shorter spadix.

BRAZIL. PARÁ: Rio Parú de Oeste (Irepecuru), *Sampaio 5158* (RB). VENEZUELA. AMAZONAS: Upper Río Negro, between Sanariapo and San Pedro, *Bunting 4249* (MO, NY); Río Orinoco, *Bunting 4248, 4250* (MO, NY); Dpt. Atures, Puerto Ayacucho Region, road to Gavilan, vic. bridge at Paseo del Diablo, 20 km SE of Puerto Ayacucho, 70--80 m, 5°33′N, 67°27′W, *Miller et al. 1596* (MO, VEN); San Pedro de Cataniapo–El Milagro, Puerto Ayacucho, 90–100 m, 6°25′N, 67°25′W, *Castillo 2229* (MO); Río Cataniapo, Las Pavas, 37 m, 06°25′N, 67°25′W, *Castillo 1650* (MO); 3 km downstream from damsite, 45 km SE of Puerto Ayacucho, 200–300 m, 05°35′N, 67°15′W, *Steyermark et al. 122191* (VEN), *122268* (MO, VEN); Puerto Ayacucho–Sanariapo, 12 km E of highway, less than 100 m, *Croat 55038* (MO); San Ferdinando de Atabapo (cultivated), *Braun 5* (VEN); Dpt. Río Negro, Cerro Neblina, 140 m, 00°50′N, 66°10′W, *Croat 59319* (AAU, B, CAS, COL, F, INPA, K, M, MO, MY, US, VEN), *Gentry & Stein 46520, 46862* (MO), *Liesner 15660* (MO), *Plowman & Thomas 13672* (MO); SW side of Cerro Neblina, 200 m, 0°49′25″N, 66°9′45″W, *Nee 30826* (MO); Río Baría, 80 m, 1°05′N, 66°25′W, *Davidse & Miller 26842* (VEN); Río Mawarinuma, 0–2 km N of Cerro Neblina Base Camp, 140 m, 0°50′N, 66°10′W, *Liesner 17384* (VEN); mouth of Cañón Grande–first major fork of Río Mawarinuma, 7 air km ENE of Puerto Chimo, 300 m, 0°50–51′N, 66°2–6′W, *Davidse & Miller 27244* (MO). BOLÍVAR: Río Suapure, Pica Caicara del Orinoco–San Juan de Manapiare, 202 km S of Caicara, 100–200 m, *Delascio & López 2797, 2812* (VEN).

Anthurium caucavallense Croat, sp. nov. TYPE: Colombia. Valle: between Cartago and San José del Palmar, 10–15 km W of Ansermanuevo, 4°49′N, 76°02′W, 900 m, *Croat 56729* (holotype, MO 3107354; isotypes, CAS, COL, JAUM, K, NY, QCA, US; live at MO). Figures 86, 87, 91, 92.

Planta epiphytica aut terrestris; internodia brevia, 1–4 cm diam.; cataphyllum anguste triangulare, uncatum; petiolus (9)15–34 cm longus, 4–10 cm diam., plus minusve D-formatus, adaxiler complanatus ad leniter sulcatus, margine elevatus, abaxiler triplinervis-quinquenervis; lamina subcoriacea, oblanceolata ad plusminusve ellipticae, (25)50–90 cm longa, (6)10–30 cm lata, nervi primariis lateralis (9)11–20 utroque; nervo collectivo e nervis infernis primariis lateralibus exoriens. Pedunculus 23–53 cm longus, 1–2-plo bis longiorus quam petiolo; spatha oblonga-lanceolata, (8)10–23 cm longa, (1)1.5–2 cm lata; spadix violaceo-purpureus, vel e violaceo-purpureo viridis, leniter contractus, (3.7)8–21 cm longus, 7–10 mm diam. Baccae violaceo-purpureae.

Epiphytic or terrestrial; stem to 20 cm long, 1–4 cm diam.; roots dense, mostly descending, ascending at uppermost nodes, pale green, densely pubescent when fresh, moderately thick, tapered, to 5 mm diam.; cataphylls coriaceous to subcoriaceous, lanceolate and hook-shaped, 7–10 cm long, acuminate at apex, olive-green turning reddish purple, heavily short lineate throughout, drying brown, persisting as a reticulum of fibers. *Leaves* spreading; petioles (9)15–34 cm long, 4–10 mm diam., erect to spreading, ± D-shaped, flattened to weakly sulcate adaxially, the margins raised, (1)3–5-ribbed abaxially, the surface pale-speckled; geniculum paler than petiole, becoming fissured transversely with age, 1–2.5 cm long; blades subcoriaceous, oblanceolate to ± elliptic, acute to acuminate at apex (the acumen apiculate), narrowly acute to subtruncate at base, (25)50–90 cm long, (6)10–30 cm wide, broadest above the middle, the margins undulate; upper surface glossy to semiglossy, medium green, lower surface semiglossy to matte, sometimes weakly to conspicuously glaucous, paler; midrib flat at base, becoming acutely raised toward the apex above, higher than broad at base below with 1–2 blunt ridges, becoming convexly raised toward the apex; primary lateral veins (9)11–

20 per side, departing midrib at (45)70–90° angle, ± straight, convexly raised above, more prominently so below; interprimary veins few, almost as conspicuous as primary lateral veins; tertiary veins flat to sunken above, weakly raised below; collective vein arising from near the apex, occasionally in the lower third or near the base, flat to scarcely sunken above, weakly raised below, 3–5 mm from margin. *Inflorescences* erect to spreading or pendent; peduncle 23–53(83) cm long, 4–6 mm diam., 1–2(5)× as long as petiole, green often tinged with maroon, terete; spathe spreading to reflexed, subcoriaceous, olive-green tinged with maroon, oblong-lanceolate, (8)10–26 cm long, (1)1.5–2 cm wide, acuminate at apex (the acumen 5–10 mm long), acute to obtuse at base; spadix violet-purple or green tinged with gray-purple, tapered, sessile or stipitate to 7 mm long in back, (3.7)8–24 cm long, 5–10 mm diam. near base, 3–5 mm diam. near apex; flowers square to 4-lobed, 2–2.7 mm in both directions, the sides straight to jaggedly sigmoid; 5–8 flowers visible in principal spiral, 13–14 in alternate spiral; tepals matte, conspicuously papillate and with droplets; lateral tepals 0.7–1.3 mm wide, the inner margins broadly convex, the outer margins 2–3-sided; pistils emergent at anthesis, densely papillate, green; stigma slitlike to ellipsoid, 0.3–0.4 mm long; stamens emerging in a regular sequence from the base, the laterals preceding the alternates by 3–12 spirals, the 3rd stamen preceding the 4th by 1–3 spirals, held above tepals in a circle around the pistil, sometimes partially inclined over and obscuring it; anthers white tinged with maroon, 0.6–0.8 mm long, 0.5–0.8 mm wide; thecae oblong, 0.3–0.4 mm wide, not at all or somewhat divaricate; pollen purplish violet fading to yellowish cream, sometimes faintly cinnamon-scented. *Infructescence* sessile with spathe persisting; to 41 cm long; spadix 20–25(44) cm long, 2.0–4.5 cm diam., with the berries scattered throughout; berries violet-purple, obovoid, truncate at apex, 4–6 mm long, 3–4 mm diam.; mesocarp mealy; seeds (rehydrated) oblong, ca. 5 mm long, 2 mm diam., adhering very closely to carpel wall throughout adaxial length.

Anthurium caucavallense is known only from the Cauca River Valley (hence the name) or its vicinity in the departments of Antioquia and Valle in Colombia, from 900 to 1,920 m. Terrestrial or epiphytic, it occurs in steep, dry, more or less exposed areas or in the understory of disturbed forest in the premontane wet forest life zone.

This species is distinguished by its hooked cataphylls, a more or less D-shaped petiole that is usually 3–5-ribbed abaxially, its primary lateral veins which often spread at a broad angle, by its violet-purple, cylindroid and weakly tapered spadix, and its violet-purple berries.

Anthurium caucavallense is most similar to *A. glaucospadix* in its leaf and petiole shape and habitat. The latter species, however, has straight cataphylls and bluish green, glaucous spadix. Other distinctive differences of *A. glaucospadix* are its obtuse to emarginate leaf apices and its primary lateral veins which always arise at a more acute angle.

Anthurium caucavallense may also be confused with *A. fendleri*, a species widespread in Colombia, but that species differs in its promptly withering spathe, thinner leaves, and early-emergent fruits.

COLOMBIA. Bogotá–San Agustín, *Bogner s.n.* (cultivated) (M). ANTIOQUIA: Mpo. Venecia, 4.2 km E of Bolobolo, road to Venecia, Hacienda La Plata, 920 m, 6°1′N, 75°48′W, *Zarucchi & Echeverry 4656* (B, M, MO); along road between Jerico and Tamesis, ca. 5 mi. NW of Tamesis, 05°42′N, 75°44′W, 1,920 m, *Croat 70035* (MO); along road from Salgar to El Dauro near border with Chocó, 05°59′N, 76°07′W, 1,830 m, *Croat 69896* (MO). VALLE: Calcedonia (bought; said to have been collected locally), *Croat 51984* (COL, DUKE, F, MO, NY, PMA, TEX); Cali–Buenaventura, Km 24, 1,750 m, *Escobar 2770* (HUA); between Loboguerrero and Cisneros, along Quebrada de Los Indios, 3°46′30″N, 76°42′W, 500 m, *Croat 62804* (K, M, MO, NY, US); Cartago–San José del Palmar, 10–15 km W of Ansermanuevo, 900 m, 4°49′N, 76°02′W, *Croat 56729* (CAS, COL, JAUM, K, MO, NY, QCA, US).

Anthurium colonicum K. Krause, Bot. Jahrb. Syst. 54(Beibl. 118): 123. 1916. TYPE: Panama. Colón: forest around Portobelo, 5–200 m, *Maxon 5801* (holotype, US). Figures 88, 89, 93.

Epiphytic; stem short, 5–7 cm diam.; leaf scars obscured by root mass and cataphylls, 1.5–1.8 cm high, 3.5–4 cm wide; roots moderately numerous, descending, green, smooth, slightly tapered; cataphylls coriaceous, erect, lanceolate, 20–36 cm long, acute to obtuse at apex with a subapical apiculum which appears hooked, green, drying tan (B & K yellow-red 9/10), persisting intact eventually as linear fibers or deciduous. *Leaves* spreading; petioles 26–90 cm long, subterete, narrowly to broadly and bluntly sulcate adaxially, the margins blunt, not raised, rounded abaxially, the surface pale-speckled; geniculum 2–6 cm long; blades coriaceous, ovate-triangular to oblong-ovate, short-acuminate at apex (the acumen to 30 mm long), broadly to deeply subcordate at base, 39–83 cm long,

(9)13–44 cm wide, broadest below the middle, the margins undulate; anterior lobe 38–76 cm long, the posterior lobes (5.5)8–17 cm long, about as broad as long; sinus arcuate, arcuate with blade decurrent on petiole or hippocrepiform in large blades; upper surface weakly glossy to semiglossy, dark green, lower surface semiglossy to glossy, paler; midrib flat to slightly angular-raised at base, gradually becoming acutely to obtusely angular toward the apex above, prominently and convexly raised below; basal veins 2–4 pairs, usually free to base, sometimes coalesced for 1–2.5 cm; posterior rib naked, sharply turned upward on outer margin; primary lateral veins 11–17 per side, departing midrib at 50–65° angle, straight to weakly arcuate, convexly raised near the midrib, becoming sunken toward the margin above, prominently and narrowly raised and paler than surface below; interprimary veins few, weakly sunken to raised above, raised below; tertiary veins obscure or weakly sunken above, weakly raised, darker than surface below; collective vein arising from one of the lowermost primary lateral veins or 1st basal vein, sunken above, raised and darker than surface below, 3–5 mm from margin. *Inflorescences* spreading to pendent; peduncle 15–48 cm long, 6–13 mm diam., 0.5 as long as petiole, terete; spathe strongly reflexed and recurled, markedly undulate, coriaceous, dark green heavily tinged with violet-purple, lanceolate to broadly lanceolate, 10–18.5 cm long, 2.5–6 cm wide, broadest just above the base, inserted at 60–65° angle on peduncle, acuminate at apex (the acumen cuspidate), acute to obtuse at base; stipe to 1 cm long; spadix green tinged with violet-purple, sessile or sometimes stipitate, tapered, (5)15.5–28 cm long, 1.2–3 cm diam., near base, 0.7–1.7 cm diam. near apex; flowers 4-lobed, 2.3–3 mm long, 2.8–3 mm wide, the sides sigmoid; 6–11 flowers visible in principal spiral; tepals matte, punctate; lateral tepals 1.4–1.9 mm wide, the inner margins broadly convex, turned up against pistil; pistils emergent to 1–3 mm, pale green, longer than the stamens at anthesis; stigma linear, ca. 0.5 mm long, droplets appearing ca. 1 week before stamens emerge; stamens emerging from the base, lateral stamens quickly followed by alternates in rapid succession, held above tepals and against pistil; filaments fleshy, transparent, 2–2.5 mm long; anthers 0.9–1.2 mm long; thecae ovoid-ellipsoid, slightly divaricate; pollen white. *Infructescence* pendent; berries orange (B & K yellow-red 8/7.5), narrowly ovoid-ellipsoid, acute at apex, ca. 10 mm long; seeds 2 per berry, pale yellow-green, brownish at apex and base, 4–4.8 mm long, 2.3–2.5 mm diam., enveloped by sticky, amber substance.

Anthurium colonicum is endemic to Panama and ranges from Veraguas to Coclé, Panamá, and Colón provinces (also in San Blas) from near sea level to 1,150 m in tropical wet and premontane rain forest.

This species is distinguished by its relatively elongate, generally subcordate leaf blades and its frequently stubby spadix with exserted stamens, but especially by its sharply pointed, early-emergent pistils, its wavy-margined spathe, and its elongate, sharply pointed, orange berries.

Anthurium colonicum is most closely related to *A. nervatum*, which has similarly veiny leaf blades, a reflexed purplish spathe, and moderately acute orange berries. The latter differs in generally having more numerous (12–30 vs. 7–12) primary lateral veins, but especially by its straight to merely twisted (but not markedly undulate marginally) spathe and its blunt pistils, emerging with the anthers, and moderately flat tepals at anthesis. In addition, the stamens of *A. colonicum* are white to yellowish when fresh, whereas those of *A. nervatum* are orange at anthesis.

PANAMA. COCLÉ: La Pintada–Coclecito, 600 m, 8°45′N, 80°30′W, *Hamilton & Davidse 2854* (MO); Llano Grande–Coclecito: S of Cascajal, Continental Divide, 800–900 m, 8°45′N, 80°25′W, *Knapp 1946* (MO); road to Coclecito, 12 mi. from Llano Grande, 200 m, 8°47′N, 80°28′W, *Churchill et al. 4169* (MO); El Copé Region, Alto Calvario, El Potroso, *Folsom & Collins 1541* (MO); Alto Calvario, 900 m, *Folsom 2493* (MO); N of Alto Calvario, N of El Copé, Limón, 800–1,000 m, *Folsom 5820* (MO); El Valle Region, Cerro Gaital, N of El Valle, La Mesa, 800–900 m, 8°40′N, 80°7′W, *Knapp & Dressler 4912* (MO); El Valle de Antón, N of Cerro Gaital, La Mesa, 800 m, *Hammel 3868* (MO); 900–1,000 m, *Croat 67235* (MO). COLÓN: Portobelo Region, 5–200 m, *Maxon 5801* (US); Río Guanche, above bridge on Portobelo Road, 3–7 km above bridge, 50–230 m, *Croat 36943* (MO); *Davidse & D'Arcy 10077* (MO); *Hammel et al. 4901, 4925* (MO); 2 mi. E of Portobelo, Nuevo Tonosí, 100 m, *Croat 33519* (B, K, MO, NY, PMA, RSA, US); Portobelo–Nombre de Dios, Río Cascajal, 0–50 m, 9°33′N, 79°38′W, *Croat 49786* (MO); 1.2 mi. beyond junction of road to Isla Grande, 9°40′N, 79°35′W, *Croat 49812* (MO); Portobelo–Nombre de Dios, Río Indio, 50 m, *Croat 33602* (B, BM, F, M, MO, PMA, US), *Croat 33640* (MO). PANAMA: Cerro Jefe, Campo Tres, 700 m, *Croat 27096* (MO); El Llano–Cartí Road, 6.8–12 km from Pan-Am Hwy., 330–450 m, *Croat 25096A* (B, F, K, MO, NY, PMA, S, SEL, TEX, US, VEN), *25174, 33760, 49114* (CAS, MO), *67344* (MO), *Mori & Kallunki 2285* (MO), *Nee et al. 8757* (MO), *Sytsma 1724* (MO, PMA); 10 mi. from Interamerican Hwy., 350 m, *Croat 33822* (MO, PMA); San Blas, 19.1 km from Interamerican Hwy., 350 m, 9°19′N, 78°55′W, *de Nevers 4976* (MO, PMA). VERAGUAS: Santa Fe Region, Cerro Tute, near Escuela Agrícola Alto Piedra, 1,070 m, *Antonio 1984* (MO); Río Santa María, N of school, 600–750 m, *Knapp & Dressler 5388* (MO); 15 km past school, Río Caloveborita headwaters, 500 m, *Sytsma & Andersson 4762* (MO); Río

Tercero Brazo, 11 km beyond Santa Fe, 650 m, *Croat 25613* (MO); Río Dos Bocas, 11 km from school, 450 m, *Croat 27544* (F, MO).

Anthurium concolor K. Krause, Notizbl. Bot. Gart. Berlin–Dahlem 11: 606. 1932. TYPE: Panama. Colón: Río Indio de Gatun, 0–300 m, *Pittier 2798* (holotype, US). Figures 90, 94–96.

Epiphytic or epilithic; stem to ca. 25 cm long, ca. 2.5 cm diam.; roots dense, spreading to erect-ascending, pale greenish white, ca. 4 cm long, 3–5 mm diam.; cataphylls narrowly coriaceous to subcoriaceous to nearly membranous, lanceolate, sometimes hooked in the upper part, weakly 1-ribbed near apex, 11–18 cm long, acuminate at apex with a subapical apiculum ca. 6 mm long at apex, drying dark brown to reddish brown (B & K yellow-red 3/10), persisting ± intact, ultimately deciduous. *Leaves* erect; petioles (2)8–16 cm long, 10–15 mm diam., erect, D-shaped to ± quadrangular, shallowly sulcate adaxially, with thin, erect margins, prominently and unevenly 3–8-ribbed abaxially; geniculum somewhat thicker and slightly paler than petiole, 1–2 cm long; blades coriaceous to subcoriaceous, usually oblanceolate to ± elliptic, sometimes narrowly obovate, acute at apex, narrowly acute to narrowly rounded (less often rounded-subtruncate) at base, (30)40–110 cm long, (13)18–36 cm wide, broadest above the middle, the margins moderately undulate; both surfaces semiglossy, upper surface medium green (B & K yellow-green 6/7.5), drying greenish to grayish brown; lower surface moderately to conspicuously paler greenish to reddish brown (B & K yellow-green 7/10); midrib flat with medial rib at base, becoming broadly acute toward the apex below, drying reddish brown; primary lateral veins 10–17 per side, departing midrib at 50–65° angle, ascending ± straight or slightly arcuate to near the margin, prominently and convexly raised above, less so below; tertiary veins scarcely visible above, slightly darker than surface below, prominulous and raised on both surfaces when dried; reticulate veins not visible below when fresh, weakly visible when dried; collective vein arising from near the apex, less prominent than primary lateral veins, 5–10 mm from margin. *Inflorescences* arching-erect to spreading; peduncle 30–75 cm long, 5–9 mm diam., 2–4.4(11)× as long as petiole, green, sometimes purple-speckled, usually subterete, sometimes 1-ribbed; spathe reflexed, subcoriaceous, green tinged with violet-purple, narrowly oblong-ovate or oblong-elliptic 5.5–14 cm long, 1.4–3.5 cm wide, inserted at 10–70° angle on peduncle, gradually to abruptly acuminate at apex, acute to obtuse at base; spadix dark purple-violet (B & K red-purple 2/5), sometimes green tinged purple-violet, sessile or subsessile, subcylindroid or weakly tapered, 5.5–16 cm long, 7–9(12) mm diam. near base, 5–7(9) mm diam. near apex; flowers rhombic, 2–3.3 mm long, 2.4–3.5 mm wide, the sides ± straight parallel to spiral, sigmoid perpendicular to spiral; 5–9 flowers visible in principal spiral, (3)6–10 in alternate spiral; tepals matte to semiglossy weakly to conspicuously and densely punctate, forming large nectar droplets on surface at anthesis; lateral tepals 2–2.3 mm wide, the inner margins straight; pistils weakly emergent, green tinged with violet-purple; stigma broadly ellipsoid, 0.5–0.6 mm long, brushlike, droplets appearing 5–8 days before stamens emerge; stamens emerging rapidly in a scattered pattern throughout, sometimes those at apex emerging first, held barely above level of the tepals, sometimes erect when dried; anthers purplish brown to purple-violet, 0.8–1 mm long, 0.8–1.1 mm wide, in a tight cluster obscuring pistil; thecae oblong-ellipsoid, ± divaricate; pollen purplish (B & K purple 6/10). *Infructescence* pendent; spathe persisting at least in early fruit; spadix to 30 cm long, 2.5 cm diam.; berries red, obovoid, 7–8 mm long, ca. 5 mm diam.; pericarp with numerous raphide cells; mesocarp transparent, gelatinous; seeds 2 per berry, white, oblong-ellipsoid, ca. 4 mm long, ca. 1.3 mm diam.

Anthurium concolor ranges from central Panama on the Atlantic slope to northern Colombia (Chocó) from sea level to 100 m in tropical wet forest and wetter parts of tropical moist forest. It is to be expected in Costa Rica in Limón Province.

This species is distinguished by its short, cylindrical, violet-purple spadix held erect at anthesis, by its tendency to form globular droplets on the tepals, by its purplish pollen, its bright red berries, and by the petioles, which are broadly sulcate adaxially and usually prominently several-ribbed abaxially.

Anthurium concolor is apparently not closely related to any other species, but has been confused with *A. salviniae* due to similarities in leaves and habit. *Anthurium salviniae* can be readily distinguished by its long-tapered, pale lavender spadix. Because of its similar leaf and petiole shape, *A. concolor* might also be confused with *A. upalaense*, but that species has a long-tapered, green spadix, a longer, recurled spathe, and orange rather than purple anthers.

COLOMBIA. CHOCÓ: hill behind Capulgana, 0–100 m, *D'Arcy 14217* (MO). PANAMA. BOCAS DEL TORO: *Carleton 377* (US). CANAL AREA: Fort Randolph, *Standley 28723* (US); Fort Sherman, *Standley 31018* (US); Matachín–Las Cascadas, *Cowell 324* (NY). CHIRIQUÍ: Barro Colorado Island, *Croat 8154* (MO); Río Provindencia, S of Colón, *Tyson & Blum 3936* (MO), *3999* (SCZ). COLÓN: Garote (cultivated: originally collected by D'Arcy), *Croat 50108* (BM, CAS, CM, MO, PMA, SEL, S); Portobelo Region, Río Indio, *Croat 33637* (B, F, K, MO, PMA, RSA, U, US); Río Indio de Gatún, 0–300 m, *Pittier 2798* (US).

Anthurium consobrinum Schott, Oesterr. Bot. Wochenbl. 5: 66. 1855. TYPE: Nicaragua. Río San Juan: along Río San Juan, *Friedrichsthal s.n.* (destroyed; Schott Aroideae #353 serves as the type). Figures 99–101.

Anthurium consobrinum var. *cuneatissimum* Engl., Pflanzenr. IV. 23B(Heft 21): 176. 1905. *Anthurium cuneatissimum* (Engl.) Croat, Ann. Missouri Bot. Gard. 70: 285. 1983. TYPE: Costa Rica. Limón: Llanuras de Santa Clara, 250 m, *Donnell Smith 6811* (holotype, B; isotypes, K, US).

Epiphytic; stem short, 1–2 cm diam.; leaf scars conspicuous, 0.7 cm high, 0.9 cm wide; roots numerous, dense, descending to spreading or ascending, white to pale green, smooth, moderately elongate and slender, blunt, to 11 cm long, 2–4 mm diam.; cataphylls subcoriaceous, lanceolate, 5.5–15 cm long, acute to caudate-acuminate at apex, light green, drying reddish brown (B & K yellow 6/2.5), persisting intact, eventually deciduous. *Leaves* erect to spreading; petioles 2.5–9 cm long, 6–10 mm diam., D-shaped, broadly sulcate adaxially, margins blunt to sharply raised, rounded abaxially, the surface pale-speckled; geniculum thicker and paler than petiole, becoming fissured transversely with age, 0.5–2 cm long; blades subcoriaceous, oblanceolate to broadly oblanceolate, long-acuminate at apex, attenuate to acute to narrowly rounded at base, 19–84 cm long, 3.5–21 cm wide, broadest above the middle, the margins broadly undulate; upper surface matte to semiglossy, medium green, lower surface semiglossy to glossy, slightly paler, drying matte, brown, occasionally greenish; midrib flat at base, becoming sharply acute-raised toward the apex above, higher than broad to round-raised at base below, becoming convexly raised toward the apex; primary lateral veins 12–18 per side, departing midrib at 40–60° angle, straight to near the margin, then arcuate and joining the margin, convexly raised above and below (more so below); tertiary veins obscure above, weakly visible below; collective vein arising from about the middle of the blade or absent, weakly sunken above, raised below, 5–12 mm from margin. *Inflorescences* erect to spreading, shorter than leaves; peduncle 20–43 cm long, 5–6 mm diam., 4–7× as long as petiole, medium green, terete; spathe spreading to reflexed, subcoriaceous, green, sometimes tinged with maroon, linear-lanceolate to oblong-ovate, 4.5–7.5 cm long, 0.8–2.5 cm wide, inserted at 30–90° angle on peduncle, abruptly acuminate at apex (the acumen inrolled), obtuse to rounded at base; spadix green to white, becoming pinkish to orange to tan to reddish violet, subcylindroid, prominently curved, 5.2–9 cm long, 0.8–1.5 cm diam.; flowers 4-lobed, 2–3.4 mm in both directions, the sides weakly to jaggedly sigmoid; 9–15 flowers visible in principal spiral, 12–16 in alternate spiral; tepals matte, greenish white turning pinkish tan; lateral tepals 1.1–1.3 mm wide, the inner margins broadly convex, turned up against pistil, the outer margins 3–4-sided; pistils early emergent, exserted to 2.2 mm, sharply pointed, pale green to white; stigma ellipsoid to circular, 0.5–0.7 mm long, becoming brushlike; stamens emerging slowly from the base, held above then retracting to surface of the tepals; filaments fleshy, colorless, 0.5–1 mm long, 0.6 mm wide; anthers white, 0.7–1 mm long, 0.7–1 mm wide; thecae narrowly ovoid, slightly divaricate; pollen white. *Infructescence* pendent; spadix to 13 cm long; berries greenish white, reddish to purplish at apex, ovoid, narrowly acute to prominently beaked at apex, ca. 10 mm long, 5 mm diam.; mesocarp clear, juicy; seeds 2 per berry, white to greenish white, oblong-ellipsoid, 3–3.4 mm long, 2 mm diam., 1.5 mm thick, enveloped by gelatinous, transparent substance extending ca. 1 mm beyond seed on both ends.

Anthurium consobrinum ranges from Nicaragua to Panama, from sea level to 850 m (mostly less than 450 m). It is a common species from tropical wet forest and premontane wet basal belt transition life zones on the Caribbean slope.

This species is distinguished by its oblanceolate blades; short, sulcate, and conspicuously sheathed petioles; whitish roots that are slender, sharply tapered, and often directed upward; spreading inflorescences with upturned nontapered spadix; the markedly protruding styles; and the berries that are greenish white at the base and reddish at the apex.

Anthurium consobrinum is probably most easily confused with *A. fatoense* of Costa Rica and Panama, differing from that species in its abaxially rounded petioles and nearly oblong spadix, and by its berry coloration. *Anthurium fatoense* has a

quadrangular petiole, a cylindroid-tapered spadix, and pale yellow or orange berries.

This species is also similar to, and may be most closely related to, *A. acutifolium*, which differs in being terrestrial or epilithic and in having a long-tapered spadix and greenish yellow berries.

COSTA RICA. WITHOUT LOCALITY: *Taylor 11593* (NY). ALAJUELA: W of La Marina, *Molina et al. 17329* (NY, US); between Naranjo and Aguas Zarcas, NE of Quesada, *Croat 46949* (MO); Zapote, *Taylor 18163* (NY); NW of Zarcero, Finca Los Ensayos, *Croat 43615* (MO); 22 km NE of Quesada by air, 4 km W of Muelle San Carlos, 10°28′N, 84°30′W, *Liesner 14173, 14174* (MO); 4 km SE of Fortuna, then 2.5 km SW on jeep road, 400–500 m, 20°29′N, 84°43′W, *Liesner et al. 15203* (MO); San Carlos, along Río Peñas Blancas, *Haber & Bello 1754* (MO); Cañas–Upala Road, 2–4 km N of Bijagua, 400–600 m, *Almeda & Nakai 4043* (MO), *Burger & Baker 9857* (DUKE, F, MO, NY), *Croat 36264* (MO), *Wilbur 20094* (DUKE); 13.8 km N of Bijagua, 100–150 m, *Croat 36423* (MO); Bijagua, *Utley & Utley 3907* (DUKE, MO); Río Zapote, 1.8–2.7 km S of Río Canalete, 100 m, *Croat 36383* (MO); Miravalles, above Bijagua, 850 m, *Gomez et al. 19065* (MO). GUANACASTE: Río Las Flores, Quebrada Desprendimiento–Quebrada Sanguijuela, Hacienda Montezuma, 450 m, *Grayum et al. 4878* (CM, CR, MO, NY); Santa María National Park, 600 m, 10°37′N, 85°17′W, *Liesner 5072* (MO). HEREDIA: E of Río Sarapiquí, Tirimbina, 150–250 m, 10°24′N, 84°7′W, *Burger & Burger 8090* (F, MO), *Proctor 32168* (LL, MO); N of Quebrada Tigre, NE of Finca El Plástico, 8 km SW of Las Horquetas, 450–550 m, 10°18′N, 84°02′W, *Grayum & Sleeper 6527* (MO); Río Peje–Río Sardinalito, Atlantic slope of Volcán Barva, 700–750 m, 10°17.5′N, 84°04.5′W, *Grayum & Jermy 6786* (MO); Finca La Selva, OTS Field Station on Río Puerto Viejo, just E of its junction with Río Sarapiquí, 100 m, *Almeda et al. 5101* (CAS), *Croat 44304* (MO), *Hammel 11627* (MO), *Jacobs 2087, 2337, 2469* (DUKE); 50 m, *Lesica & Antibus 4134* (MO), *McDowell 132, 399* (MO), *750* (DUKE, MO), *Sperry 622* (MO), *Wilbur 37240, 37624, 37730* (DUKE), *Wilbur & Jacobs 34205, 34963* (DUKE); Puerto Viejo Region, Río Sucio, 20 m, *Croat 35671, 35695* (MO); Puerto Viejo, *Burger & Stolze 5934* (PMA), *Garwood et al. 883* (BM, MO), *Taylor 4571* (NY); 4.5 km SE of bridge at Puerto Viejo, 50 m, 10°26′N, 83°58′W, *Stevens 13494* (MO); San José–Puerto Viejo, vic. Chilamente, 11.6 mi. N of Cariblanco, 10°27′N, 84°05′W, 100 m, *Croat 68360* (MO). LIMÓN: Cahuita–Limón, 0–10 m, 9°44′N, 83°2′W, *Baker & Burger 151* (BM, CAS, CM, F, MO, US); Finca Castilla, 30 m, *Dodge & Goerger s.n.* (MO); 29 air km W of Tortuguero, Hacienda Tapezco and Hacienda La Suerte, 40 m, 10°30′N, 83°47′W, *Davidson et al. 6723, 6768* (MO), *Davidson & Donahue 8413, 8461, 8733* (MO); Parque Tortugero, 40 m, 10°10′N, 83°34′W, *Robles 1159, 1233* (MO); 10–80 m, 10°31′N, 83°01′W, *1518* (MO); between Barra del Colorado and ocean beach, 0–2 m, 10°47′N, 83°35′W, *Stevens 24138A* (MO); hills 2 air km SSE of Islas Buena Vista in Río Colorado, 14 air km SW of Barra del Colorada, 10–120 m, 10°40′N, 83°40′W, *Davidse & Herrera 31058* (MO, U); Cerro Coronel, E of Laguna Danto, 20–170 m, 10°41′N, 83°38′W, *Stevens 23654* (MO); Río Colorado, 2 km upstream from downstream branch of Caño Bravo, 5 m, 10°43′N, 83°40′W, *Stevens 24032* (MO). NICARAGUA. CHONTALES: 4 km NW of Santo Domingo, 280 m, 12°17′N, 85°6′N, *Grijalva et al. 3811* (MO). GRANADA: N of Mombacho, San José, 700–800 m, 11°49′N, 85°58′W, *Sandino 2508* (MO). MATAGALPA: NE side of Cerro Peñas Blancas, Matagalpa–Waslala, *Grijalva & Moreno 3461* (MO). RÍO SAN JUAN: 20 km NE of El Castillo, Río Indio watershed, 200 m, *Neill 3421* (MO); 3 km from confluence of Río San Juan and Río Sábalo, Sábalo, 40–50 m, *Araquistain 3229* (MO); 2 km NW of Sábalos, 70 m, 11°2′N, 84°29′W, *Moreno 23281* (MO); 2 km W of Santa Eduviges, Río Sabalós, 70–80 m, 11°3′N, 84°29′W, *Moreno 23017, 23037* (MO); Caño Chontaleño, 20 km NE of El Castillo, 200 m, *Neill 3332, 3376, 3420* (MO), *Neill & Vincelli 3488* (MO, TEX), *3622* (MO); Cerro El Gigante, Castillito–Caño de Oro, 10 m, 10°43–44′N, 84°54′30″W, *Martínez 2167* (MEXU); Río Santa Cruz at confluence with Río San Juan, 42 m, 11°2′N, 84°24′W, *Moreno 25532* (MO). ZELAYA: 6.3 km S of bridge at Colonia Yolaina, SW of Colonia Naciones Unidas, 200–300 m, 11°36′N, 84°22′W, *Miller & Sandino 1100* (MO); *Stevens 4819, 4826, 6411, 6412* (MO); 1.3 km SE of intersection with road Nueva Guinea–Colonia Verdún, road to Colonia Yolaina, Colonia La Esperanza, 180–200 m, 11°40′N, 84°26′W, *Stevens 6308* (MO); road to Colonia Yolaina and Colonia La Esperanza, 180–200 m, *Vincelli 166, 168* (MO); 1.5 km SE of Estación Experimental "El Recreo," *Soza et al. 448* (MO); Colonia Yolaina, Nueva Guinea, 300 m, 11°38′N, 84°21′W, *Araquistain 3126* (MO); 1 km N of El Zapote, 6 km S of Colonia Verdún, 250–300 m, 11°34′N, 84°24′W, *Nee & Vega 27907* (MO); Bluefields, N of Base Camp, *Proctor et al. 26913, 27010* (LL, MICH, NY, US); Caño Costa Riquita, 1.8 km SW of Colonia Naciones Unidas, 150–180 m, 11°43′N, 84°18′W, *Stevens 4966, 5058* (MO); Caño Monte Cristo, 10 m, 11°33′N, 87°48′W, *Moreno & Sandino 14704* (MO); Cerro Las Nubes, 10–60 m, 11°37′N, 83°52′W, *Moreno 14975* (MO); Las Faldas, 40–60 m, 11°36′N, 83°51′W, *Moreno 14811* (MO); German Pomares–Las Benitas, 100 m, 11°36′N, 83°51′W, *Moreno & Sandino 14878, 14923* (MO); 1 km before German Pomares, 10 m, 11°35′N, 83°51′W, *Moreno 14840* (MO); Caño Monte Cristo and Caño El Consuelo confluence, 10 m, 11°35′N, 83°51′W, *Moreno 15033* (MO); Quebrada La Talolinga, 170 m, 11°51–52′N, 84°26–27′W, *Miller & Sandino 1176, 1178* (MO); Río Punta Gorda, Atlanta, "La Richard," 20–30 m, 11°32′N, 84°5′W, *Moreno & Sandino 12967, 13008, 13114* (MO); Atlanta, "La Richard," Loma San Jorge, 150–160 m, 11°31′N, 84°4′W, *Moreno & Sandino 13041* (MO); Río Rama, Caño Zamora, 10 m, 11°57′N, 84°16′W, *Stevens 8861* (MO); Salto La Oropendola, 15–25 m, 11°57′N, 84°17′W, *Stevens 8954* (MO). PANAMA. COLÓN: between Portobelo and Madre de Dios, 1.2 mi. beyond junction to Isla Grande, 9°40′N, 79°35′W, *Croat 49812* (MO). VERAGUAS: Santa Fe Region, Cerro Tute, vic. Escuela Agrícola Alto Piedra, 600–1,400 m, 8°30–32′N, 81°07′W, *Knapp & Kress 4357* (B, MO), *Knapp & Dressler 5435* (B, MO), *McPherson 10722* (MO).

Anthurium coriaceum G. Don in Sweet, Hort. Brit. ed. 3. 633. 1839. Figures 97, 98, 102.

Pothos coriacea Graham, Edinb. Phil. J. 14: 353. 1826, non Salisb. (1796). TYPE: Brazil. Rio de Janeiro: *Harris s.n.* (cult. Kew).

Anthurium coriaceum [Endlicher, Gen. Pl. 240. 1837, comb. not made under ICBN Art. 33.1] G. Don in Sweet, Hort. Brit. ed. 3. 633. 1839.
Anthurium glaucum Schott, Wiener Z. Kunst 1829(3): 828. 1829, nomen nudum.
Anthurium glaucescens Kunth, Enum. Pl. 3: 73. 1841. TYPE: Origin unknown (type not designated).
Pothos glaucus Schott ex Kunth, Enum. Pl. 3: 73. 1841, invalidly published in synonymy.
Pothos subcaulescens Vell. Conc., Fl. Flum. Archivos do Mus. Nac. 390. 1881. TYPE: Brazil. exact location unknown. Plate 122 in Flora Flumiensis 1825 [1829] serves as the type.
Anthurium rubriflorum Engl., Bot. Jahrb. Syst. 25: 399. 1898. TYPE: Brazil. Rio de Janeiro: Gavea, Glaziou 71 (cult. Berlin) (holotype, B).
Anthurium subcaulescens (Vell. Conc.) Stellfeld, Arq. Mus. Paran. 8: 177. 1950.

Terrestrial or epilithic, sometimes epiphytic; stem less than 20 cm long, 1.5–3.5 cm diam.; roots mostly descending, to 5 mm diam.; cataphylls coriaceous, unribbed, broadly lanceolate, 12–14 cm long, acute to obtuse at apex, drying straw-colored, becoming brown toward base, persisting semi-intact. *Leaves* erect-spreading; petioles (3)19–60 cm long, (4)10–15 mm diam., terete, sometimes obtusely flattened adaxially, the surface sometimes pale-speckled; geniculum moderately thicker and paler than petiole, 1–2.5 cm long; sheath 4–5.5 cm long; blades coriaceous, broadly elliptic to somewhat oblong, sometimes somewhat lanceolate or oblanceolate, acute to rounded and minutely apiculate at apex, acute to obtuse or rounded (rarely shallowly cordate) at base, (35)60–110 cm long, (6)15–28(39) cm wide, broadest usually above the middle, the margins moderately undulate; upper surface matte to weakly glossy, medium green, lower surface semiglossy, slightly paler; midrib above flat to broadly convex at base, becoming convexly to acutely raised toward apex, prominently convex below; primary lateral veins numerous, departing midrib at (40)50–70(80)° angle, straight to slightly arcuate to the collective vein, weakly sunken to weakly raised and obscure above, similar but more visible below, raised above and below when dried; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins prominulous above and below on drying; collective vein arising near the base, equally as prominent as primary lateral veins, 5–20(30) mm from margin. *Inflorescences* erect; peduncle 11–44 cm long, (3)5–9 mm diam., (0.2)0.5–1.7(3.6)× as long as petiole, terete; spathe erect, coriaceous, green, broadly lanceolate-elliptic, (7.5)10–24 cm long, (1.7)2.5–4.3 cm wide, broadest near the base, acute to acuminate at apex, acute at base; spadix pale purplish to maroon, sessile, tapered, erect, straight to slightly curved, 10–31 cm long, 8–12 mm diam. midway, 4–5 mm diam. near apex; flowers rhombic, 2.5–3.1 mm long, 1.8–2 mm wide, the sides straight to weakly sigmoid; 13–23 flowers visible in principal spiral, 8–14 in alternate spiral; tepals matte, smooth; lateral tepals 1.6–2 mm wide, the outer margins 2-sided, the inner margins rounded; stigma oblong-ellipsoid, 0.5 mm long, depressed medially; anthers 0.5–0.7 mm long, 0.6–0.7 mm wide, inclined over and obscuring pistil; thecae ovoid-oblong, slightly or not divaricate; pollen pale yellow on drying. *Infructescence* erect; spathe persisting; spadix to 18 cm long, 2 cm diam., with the berries scattered throughout; berries dirty white to pale lavender, greenish at apex, obovoid-oblong, truncate at apex, 7 mm long, 5 mm diam., the pericarp with raphide cells; seeds 2 per berry, ovoid-ellipsoid, 4.5–5 mm long, 3–3.5 mm wide, 1.7–2 mm thick, flattened on one side, oblique and with a short, hooked appendage at apex.

Anthurium coriaceum is endemic to coastal southeastern Brazil, ranging from central Espírito Santo to Guanabara with a single outlying collection on Dos Corais Islands off the coast of Paraná State. It is expected in some of the few remaining natural areas along the coast between Rio de Janeiro and Paraná states. The species occurs terrestrially, or on rocks, less often epiphytically, in dry areas on windward slopes below 500 m.

This species is readily distinguished by its large, coriaceous, green-drying, more or less matte leaf blades with numerous primary lateral veins that are as conspicuous as the interprimary veins, and a collective vein which arises from near the base and is remote from the margin. The peduncle may be shorter or slightly longer than the petioles.

Anthurium coriaceum is not closely related to or confused with any other species. In some respects (especially venation), it is like members of sect. *Urospadix*, which are especially common in this part of Brazil, but has involute vernation and thus shows its affinity with sect. *Pachyneurium*.

BRAZIL. WITHOUT LOCALITY: *Glaziou 71* (B (cult. Berlin)), *15575, 16519* (C), *s.n.* (F, US), *Warming s.n.* (C), *Widgren 1081* (S), *Lassen s.n.* (C). ESPIRÍTO SANTO: along Hwy. BR-259 between Colatina and Vitória, at km 38.5 from junction of BR-259 and BR-101, 14.2 km E of Colatina, 19°33′S, 40°36′W, 160 m, *Croat 61907* (MO, R); Domingos Martins, Fazenda Kautsky, 550–860 m, *Croat 61815* (R). GUANABARA: Barra da Tijuca, *Pabst & Klein 5228* (B); Gavea, *Ule 4872* (HBG). PARANÁ: Ilha dos Corais, *Hatschbach 32538* (MO, NY). RIO DE JANEIRO: without locality, *Glaziou 17335* (K); Pão de Açúcar, Costão, 200 m, *Carauta 429* (GUA), *Casari & Vilaca 105* (GUA); Leme, Morro do Leme, *Kennedy 838* (F); Mpo. Niteroi, Alto Moinas, Praia de Itaipucu, 100–250

m, 22°53′S, 43°07′W, *Croat 53757* (CM, K, MO, NY, RSA), *53781* (MO); Itaipu, Morro das Andorinhas, *Araujo & Vilaca 3847* (GUA); Represa do Camorim, *Araujo 3751* (GUA); road to Represa do Camorim, Estrada da Boca do Mato, Vergem Grande, *Rocha 151* (GUA); Cabo Frio, Arraial do Cabo, Pontal beach, *Segadas-Vianna et al. 665* (NY). SÃO PAULO: cultivated at Floricultura Campina Hda., *Hutchison 8850* (MO).

Anthurium cotobrusii Croat & R. A. Baker, Brenesia 16(Suppl. 1): 43. 1979. TYPE: Panama. Chiriquí: above San Félix, along mining road, 18–27 mi. off Pan-Am Hwy., 1,200–1,500 m, *Croat 33058* (holotype, MO 2381190-91; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, GH, K, L, M, MBM, MEXU, NY, P, PMA, RSA, SEL, US, W). Figures 107, 108.

Terrestrial or often epilithic; stem usually less than 15 cm long, 1–3 cm diam.; roots descending, greenish or grayish brown, smooth to weakly pubescent, moderately thick and elongate, to 6 mm diam.; cataphylls subcoriaceous, lanceolate, 4.5–11 cm long, acute at apex, green, sometimes tinged with purplish, drying light brown, persisting semiintact, eventually as fine linear fibers. *Leaves* erect to spreading; petioles 15–65 cm long, 4–7 mm diam., ± terete, weakly sulcate to flattened adaxially, rounded abaxially; geniculum thicker than petiole, (1)3–5 cm long; blades subcoriaceous, narrowly ovate to triangular, long-acuminate at apex (the acumen downturned, weakly apiculate), shallowly and broadly cordate at base, 16–65 cm long, 9.5–33 cm wide, broadest at base, the margins weakly undulate; anterior lobe (13)18–30(37) cm long, the posterior lobes (5)7–13(15) cm long, directed upward and slightly inward, narrowly rounded at apex; sinus arcuate to broadly parabolic when flattened, hippocrepiform when not, (4)7–9 cm deep; upper surface semiglossy, dark to medium green, lower surface glossy to semiglossy, conspicuously paler, both drying matte to weakly glossy, yellowish green; midrib obtusely raised at base, becoming more sharply raised and then sunken at apex above, obtusely to convexly raised and more prominent below; basal veins 3–5 pairs, all free to base or 3rd–4th coalesced 4–6 cm, weakly raised to flat above, weakly raised and darker than surface below; posterior rib naked, gradually curved to almost straight, turned up on outer margin; primary lateral veins 4–8 per side, departing midrib at 50–60° angle, broadly arcuate, sharply to weakly raised or weakly sunken above, weakly raised to flat and darker than surface below; interprimary veins obscure above, flat and darker than surface below; tertiary veins obscure above, weakly visible below; reticulate veins obscure above and below; collective vein arising from one of the uppermost basal veins or one of the lowermost primary lateral veins, sunken above, slightly raised and darker than surface below, almost as prominent as primary lateral veins, 3–8 mm from margin. *Inflorescences* erect-spreading; peduncle (4)20–60 cm long, 4–10 mm diam., (0.7)1–1.7× as long as petiole, terete; spathe reflexed, subcoriaceous, green to pale green or green with purplish veins or heavily suffused with purple on inner surface, sometimes tinged with purple only at base, ovate to narrowly ovate, weakly boat-shaped to flat, (2.5)5–15 cm long, (1.7)2.7–4.5 cm wide, inserted at 60–90° angle on peduncle, acuminate at apex (the acumen inrolled), acute to rounded or shallowly cordate at base; stipe 1–2 cm long in front, 2–6 mm long in back; spadix green to brownish green to dark purple-violet, cylindroid to weakly tapered, erect to curved, (2.5)5–25 cm long, 7–15 mm diam. near base, 3–7 mm diam. near apex; flowers ± 4-lobed, 3.5–5 mm long, 3.5–4 mm wide; 3–6 flowers visible in principal spiral, 7–10 in alternate spiral; tepals sparsely punctate, more densely so near the margins, semiglossy to matte, the inner margins broadly convex; pistils emergent, matte, green; stigma linear, purple-violet or green, ca. 0.6 mm long, with brushlike papillae; droplets appearing 1–3 weeks before stamens emerge, sometimes persisting when 1st and 2nd stamens are opening; stamens weakly exserted, in a tight cluster above pistil; filaments whitish, soon retracting, 0.4 mm long, 1 mm wide; anthers orange to yellowish, 0.6–0.9 mm long, 1 mm wide; pollen pale orange fading to white, yeasty-scented. *Infructescence* erect spreading; spathe persisting; spadix 12–18 cm long, 1.5–2 cm diam.; berries pale orange (B & K yellow-red 8/7.5), obovoid, darker and rounded at apex with radial ridges, 12–15 mm long, 8–11 mm diam.; mesocarp juicy, orange; seeds usually 2 per berry, oblong-ellipsoid, 6.5–7.5 mm long, 2.5–4 mm diam., encased in flattened, translucent envelope that projects up to 3 mm beyond the apex of the seed and up to 1 mm beyond the lateral margins.

Anthurium cotobusii is found in Costa Rica and Panama, in premontane wet forest at elevations of 600 to 1,850 m.

This species is most easly distinguished by its subcoriaceous leaves which have more or less obscure reticulate veins when dried, and by its prominently tapered, violet-purple spadix with stamens in tight clusters. In the dried state the flowers have

their tepals turned somewhat upwards, which, in conjunction with the clustered stamens, gives the spadix a rough appearance. Other diagnostic features are the primary lateral veins often free to the margin in the basal half of the blade, the thick, grayish roots that are densely long-pubescent on drying and the early emergent berries that are quadrangular with prominent ridges radiating from the center to the corners.

Anthurium cotobrusii is an atypical member of sect. *Pachyneurium*, probably related to other cordate and subcordate, orange-fruited species such as *A. colonicum*, *A. nervatum*, *A. ranchoanum*, and *A. watermaliense*.

Specimens of *A. cotobrusii* with longer posterior lobes can be confused with *A. watermaliense*, but that species is distinguished by its early emergent pistils held above the tepals before anthesis, and by its often persistently long-exserted stamens.

The species was placed in sect. *Cardiolonchium* by Croat & Baker (1979) and later in sect. *Belolonchium* (Croat, 1983), but was confirmed as a member of sect. *Pachyneurium* by its involute vernation.

COSTA RICA. PUNTARENAS: Las Cruces–Neily, Fila de Cal, *Gómez 19649* (CR, MO); Río Coto Brus, 23 km N of La Unión, Panama border, *Croat 26674* (MO); San Vito de Coto Brus–Villa Neily, Fila de Cal, Cuesta Fila de Cal, 300–600 m, 8°41′N, 82°56.5′W, *Hammel 14160* (MO); Cordillera de Talamanca, Tres Colinas, 1,800–1,850 m, 9°7′N, 83°4′W, *Davidse et al. 25652* (MO); Cerro Frantizius–Cerro Pittier, Río Canasta, 9.5 air km NW of Agua Caliente, 1,500–1,600 m, 9°2′N, 82°59′W, *Davidse et al. 28366* (MO); Cerro Pando, 1,000–1,800 m, 8°55′N, 82°45′W, *Barringer & Gómez 1617* (F); Refugio de Fauna Silvestre, Peñas Blancas de Esparza, 1,000–1,400 m, 10°7′ 50″N, 84°40′25″W, *Herrera et al 295* (DUKE, F, MO, TEX, US); cultivated at Las Cruces Botanical Garden, 1,300 m, *Croat 44452* (MO); originally from Las Alturas, *Croat 44387* (MO). PANAMA. CHIRIQUÍ: above San Félix along mining road 18–27 mi. off Pan-Am Hwy., above Chamí or turnoff to Escopeta, 1,200–1,500 m, *Croat 33058* (AAU, B, CAS, CM, COL, CR, DUKE, F, GH, K, L, M, MBM, MEXU, MO, NY, P, PMA, RSA, SEL, US, W), *33147A*, *33152* (MO); Cerro Colorado, 7.6 km from main road, 1,450–1,750 m, *Folsom et al. 4840* (MO); 17 km NE of San Félix, 13–14 km by road NE of bridge over Río San Félix, 1,000 m, *Nee 10699* (MO); Cerro Hornito, beyond Gualaca, 2–3 km E of Finca Linares, vic. Planes de Hornito, 1,400–1,900 m, *Croat 48850* (CM, COL, CR, ENCB, LE, M, MO, U); 1,750–1,900 m, 8°41′N, 82°10′W, *Croat 67983* (MO).

Anthurium cowanii Croat, sp. nov. TYPE: British Guiana. Kaieteur Plateau, forest along Potaro River, ca. 1 mi. above Kaieteur Falls, 470 m, *Cowan & Soderstrom 2230* (holotype, BH; isotypes, K, NY, US). Figure 103.

Planta epiphytica; internodiis brevibus, caule 1–1.5 cm diam.; cataphyllum persistens semi-intactum; petiolus 8.5–13 cm longus, 7–10 mm diam., D-formatus; lamina oblanceolata, 50–90 cm longa, 13.5–30 cm lata; pedunculus 49–63.5 cm longus, 3–7 mm diam.; spatha 9–16 cm longa, 1.5–2.5 cm lata; spadix stipitatis, (9)15–18(21) cm longis, 6–7(10) mm diam., atropurpureus-rubescens ad brunneo-rubescens. Baccae ignotae.

Description based on dried material only. Epiphytic; stem ca. 1–1.5 cm diam.; roots dense, numerous, grayish brown, somewhat pubescent, ca. 2–3 mm diam.; cataphylls apparently subcoriaceous, at least 8 cm long, acute at apex, brown (B & K yellow 4/2.5), persisting semi-intact, eventually as fine linear fibers; petioles 8.5–13 cm long, 7–10 mm diam., D-shaped, apparently sulcate adaxially, with the margins prominently raised, probably rounded abaxially; geniculum slightly thicker than petiole, 0.8–1.7 cm long; sheath (2.5)5.7–6.5 cm long; blades coriaceous, oblanceolate, acute to shortly acuminate at apex, narrowly rounded to obtuse at base, 50–90 cm long, 13.5–30 cm wide, broadest above the middle, the margins apparently undulate; both surfaces semiglossy to weakly glossy, grayish green to brownish green; midrib convexly raised above, slightly paler than surface, prominently convex to higher than broad below, somewhat darker than surface; primary lateral veins 9–16 per side, departing midrib at 25–50° angle, straight, becoming somewhat arcuate toward the apex, prominently convex above and below, more so below; interprimary veins not present; tertiary veins prominulous, raised above and below; reticulate veins weakly raised; collective vein arising from near the apex, raised above and below, 3–11 mm from margin. *Inflorescences* with peduncle 49–63.5 cm long, 3–7 mm diam., 6.1–7.5× as long as petiole, probably terete; spathe apparently erect to spreading, coriaceous, green, oblong-lanceolate, 9–16 cm long, 1.5–2.5 cm wide, broadest near the base, shortly acuminate at apex (the acumen inrolled, 7–15 mm long), acute at base; stipe 1.5–4(7) cm long in front, 0.5–1.5(2.5) cm long in back; spadix dark purple-red to brown-red, long-tapered, somewhat curved, held at 150–165° angle from peduncle, (9)15–18(21) cm long,

6–7(10) mm diam. near base, 4–6 mm diam. near apex; flowers rhombic, 4–4.6 mm long, 2.5–2.8 mm wide, the sides straight; 7–8 flowers visible in principal spiral, 5–6 in alternate spiral; tepals minutely papillate, semiglossy on drying; lateral tepals 2.3–2.8 mm wide, the inner margins broadly rounded, the outer margins 2-sided; pistils minutely papillate; stigma slitlike, 0.4–0.5 mm long; anthers 0.4–0.5 mm long, 0.5–0.6 mm wide, contiguous, obscuring pistil; thecae oblong, not at all or slightly divaricate; pollen fading to white. Fruit unknown.

Anthurium cowanii is known only from the Kaieteur Plateau in gallery forest along the Potaro River in Guyana at 470 m, where it was reported as an epiphyte in a premontane moist forest life zone (though the area is mostly savanna).

This species is characterized by its large, oblanceolate and short-petiolate leaf blades which dry greenish gray above and more brown and semiglossy below. Also, the dark purple-red, tapered spadix on a peduncle much longer than the petioles is an important distinctive feature. *Anthurium cowanii* is not likely to be easily confused with any other species, but *A. loretense* and *A. vaupesianum*, from lowland western Amazonia, may bear a resemblance in the color of the leaf blades on drying.

Anthurium cowanii has been cultivated at the New York Botanical Garden. An herbarium voucher at NY, prepared in 1948, was made from a living plant brought back as *Maguire & Fanshawe 26173*, from the Potaro River Gorge, but no field voucher has been located. The cultivated specimen resembles field-prepared specimens of *A. cowanii* quite well, but leaf blade shape is more obovate-oblanceolate (vs. oblanceolate).

The species is named in honor of Richard S. Cowan, who collected in the Guiana region in the early 1950s and early 1960s and who, with T. R. Soderstrom, collected most of the known material of *A. cowanii*.

GUYANA. Kaieteur Plateau, Potaro River, ca. 1 mi. above Kaieteur Falls, 470 m, *Cowan & Soderstrom 2230* (BH, K, NY, US), *1758* (BH, US); (cultivated), *Maguire & Fanshawe 26173* (NY).

Anthurium crassinervium (Jacq.) Schott, Weiner Zeitschr. 1825: 828. 1825. *Pothos crassinervia* Jacq., Icon. Pl. Rar. 3 (1793), t. 609, Coll. 4. 122. TYPE: t. 609 serves as the type. Figures 104, 105, 109, 110.

Anthurium ellipticum K. Koch & Bouché, Ind. Sem. Hort. Berol. App. 6. 1853. TYPE: Venezuela. Caracas, *Gollmer s.n.* (lectotype, B; photo seen (Field Mus. Neg. #F-011915)).

Anthurium rugosum Schott, Oesterr. Bot. Z. 8: 387. 1858. TYPE: Venezuela: Caracas, *Gollmer s.n.* (B, lectotype; photo seen (Field Mus. Neg. #F-012065)).

Anthurium egregium Schott, Prodr. 475. 1860. TYPE: Schott Aroideae 486 (microfiche #13 A 10) serves as the lectotype (W).

Anthurium fontanesii Schott, Bonplandia 10: 347. 1862. TYPE: Locality unknown, from a cultivated source; Field Museum Photo 29816 serves as the type.

Anthurium preussii Engl., Pflanzenr., IV. 23B(Heft 21): 68. 1905. TYPE: Venezuela. Carabobo: Porto Cabello, *Preuss 1552* (holotype, B; isotype, BM).

Epiphytic, epilithic or terrestrial, sometimes colonial; stem short, 2.5–4 cm diam.; roots dense, ascending, smooth; cataphylls subcoriaceous, 7–13 cm long, acute at apex, drying medium brown (B & K yellow 4/7.5), persisting ± intact, weathering into reticulum of fibers. *Leaves* erect to spreading; petioles 3–33.5 cm long, 4–11 mm diam., D-shaped to quadrangular or thicker than broad, broadly and shallowly sulcate to V-sulcate, rarely narrowly sulcate adaxially, the margins acute, rarely inclined inward, flattened to rounded or 3–5-ribbed abaxially; geniculum somewhat thicker and paler than petiole, 0.8–2 cm long; blades moderately coriaceous, oblanceolate, gradually acuminate or rarely rounded at apex, acute to somewhat obtuse at base, 25–142 cm long, 11–52 cm wide, broadest usually above the middle, the margins undulate; both surfaces matte to semiglossy, slightly paler below, often pale-pustulate and/or with pale or dark punctations; midrib flat with a conspicuous medial rib near the base above, becoming acutely raised near the middle, sharply raised below, sometimes 3-ribbed at base; primary lateral veins 6–14 per side, departing midrib at 40–70° angle, ± straight or arcuate to the margin, prominently raised near the midrib above, then sunken and merging with margin, raised below, drying raised and paler on both surfaces; interprimary veins not apparent; tertiary veins flat and slightly visible above, visible and darker than surface below; collective vein arising in the upper ⅓ or in the upper ¼ of the blade, prominulous when dried. *Inflorescences* erect to spreading; peduncle (13)20–98 cm long, 5–12 mm diam., 1–3(5)× as long as petiole, terete, sometimes ribbed near the base of spathe; spathe spreading to reflexed, moderately thin, green, sometimes tinged with purple, lanceolate, 8–12.5 cm long, 1.5–2 cm wide, broadest near the base, often decurrent at base; spadix dark purple or violet to green or green tinged with purple, tapered, sessile or stipitate to 12 mm, (6)12–

33 cm long, 7–10 mm diam. near base, 4–7 mm diam. near apex; flowers rhombic to 4-lobed, 2.4–3.1 mm long, 1.6–2.8 mm wide, the sides jaggedly sigmoid; 7–10 flowers visible in principal spiral, 5–10 in alternate spiral; tepals matte; lateral tepals 1.2–1.5 mm wide, the inner margins rounded, tinged with violet-purple; pistils emergent, violet-purple; stigma linear, 0.5 mm long; stamens emerging from the base of the spadix, laterals emerging to midway followed by alternates in rapid succession, arranged in a circle around the pistil just above the tepals; anthers pale orange (B & K yellow-red 8/7.5) 0.7 mm long, 1 mm wide; thecae ovoid, slightly divaricate; pollen pale orange, white when dried. *Infructescence* pendent; berries red, ovoid, basally attached to spadix by 4 tepalar fibers, 7.6–8.2 mm long, 3–3.5 mm diam. on rehydration; pericarp studded with raphide cells; seeds 1–2 per berry, pale yellowish, with raphide cells, ellipsoid, 3.6–4.4 mm long, 1.6–2.2 mm diam., 0.8–1.6 mm thick, with a mucilaginous apical appendage.

Anthurium crassinervium ranges throughout northern Venezuela in the states of Aragua, Carabobo, Falcón, Lara, Mérida, Miranda, Portuguesa, Táchira, Trujillo, Yaracuy, Zulia, and the Distrito Federal, from sea level to 1,800 m. It has also been found in Colombia in the departments of Cesar, Guajira, Magdalena, and Santander from 400 to 1,600 m, and on Curaçao in the Netherlands Antilles at 350 m. The species is ecologically quite variable, occurring in tropical moist, tropical dry, premontane wet, premontane wet (transitional to warm), premontane moist, premontane dry, subtropical dry, and subtropical thorn forest transitional to subtropical dry forest.

Although quite variable in size, *A. crassinervium* can be recognized by its lanceolate, usually acute at the base blades with undulate margins and often with pustular or pale to dark punctations on the abaxial surface, by its lanceolate and sometimes early-deciduous spathe, tapered spadix, and red berries with the seeds attached apically to the carpel wall by a mucilaginous appendage.

Some exceptional collections that should be mentioned are tentatively placed here. Two, *Bunting & Holmquist 4327* and *4328*, from Bolívar State in Venezuela (the only collections known from Bolívar), are quite typical for the species except for the unusually large leaf blade size and the unusually high number of flowers in the primary spiral (11 flowers per spiral). Another collection of note is *Bunting 4397*, from Táchira, with 13 flowers in the primary spiral, and a spathe 5 cm broad. The overall size of the latter plant is reported to be unusually large. Several collections from lower elevations north of the Cordillera de la Costa, especially those from near Cata in Aragua, Venezuela (*Bunting 2197, 2198, 2199, 2200, 4353, 13501, 13508, 13509, 13510, 13511*), are unusual in having the petioles narrowly sulcate and sometimes with the margins convergent adaxially. While this material is interpreted by Bunting (pers. comm.) as *A. ellipticum*, the original description of *A. ellipticum* makes no mention of petiole shape, and subsequent illustrations by Schott (1984) and Engler (Engler's Araceae Illustrations No. 249) show the petiole as shallowly and broadly sulcate with inconspicuous margins adaxially. Petiole shape in *A. crassinervium* is highly variable, and the Aragua specimens exhibit just one of the extremes. Curiously, in his 1905 revision, Engler illustrated *Anthurium ellipticum* (fig. 22) as having a prominently sulcate petiole with the margins curved inward. There is no indication that *A. ellipticum* is out of the range of variation in *A. crassinervium*; however, the illustration of *A. ellipticum* in *Das Pflanzenreich* represents a plant like those mentioned above from near Cata. These may represent a distinct taxon, perhaps a subspecies of *A. crassinervium*. In addition to the petiole cross-section differences, these plants also have longer, more tapered spadices, and are always epilithic or terrestrial (often in sand). This taxon, if recognized, would probably include *A. preussi*, described from a similar area near Puerto Cabello, and perhaps also *A. fontanesii*, but not *A. ellipticum*. Petiole shape in *A. crassinervium* is highly variable, and this represents just one of the extremes.

Anthurium crassinervium is closely related to *A. wagenerianum*, but the latter generally has a short, stout spadix and a short, broadly lanceolate spathe. Its leaf blade margins are minutely undulate in dried specimens, instead of wavy, and are apically cuspidate, instead of acute. Furthermore, the lower leaf epidermis in dried specimens of *A. wagenerianum* is not highly light-reflective at low magnifications, and the concentric epidermal cell pattern observed in *A. crassinervium* is not apparent. The fruits of *A. wagenerianum* are distinctive as well. See that species for further details. Engler distributed several specimens that he determined as *A. wagenerianum*, but which have a markedly tapered spadix like that of *A. crassinervium* and therefore have been included there.

The range of *A. crassinervium* overlaps that of another species which possibly could be confused with it, namely *A. fendleri*, but the latter can be distinguished by its usually thinner blades that are

usually narrowly rounded to subcordate at the base, and by its thin, caducous spathe.

Anthurium bonplandii subsp. *guayanum* might also be confused with *A. crassinervium*, as both have similarly shaped leaves that are pustular or punctate abaxially. The petiole of the former is C- or D-shaped and rounded abaxially, while the latter usually has quadrangular petioles which are usually ribbed abaxially. The berries of *A. bonplandii* subsp. *guayanum* are rather dry upon rehydration, and its seeds are attached by a band of fibers. *Anthurium crassinervium*, in contrast, has the more typical seed for sect. *Pachyneurium*, attached to the berry by a mucilaginous appendage.

Pothos crassinervia Jacq. was depicted in Curtis's Botanical Magazine (t. 2987) by J. D. Hooker in 1830 and was said to have come from Demerara (Guyana); however, this was a living collection sent by James Fraser, Esq., and was possibly not locally collected. To date there are no indications the species occurs in the Guianas.

Lectotypification has been necessary in the cases of *A. crassinervium*, *A. ellipticum*, *A. rugosum*, *A. egregium*, and *A. fontanesii*. In the first case, Jacquin clearly described his new species, *Pothos crassinervia*, in 1790, while his illustration, here lectotypified, was not published until 1793. In the second case, Koch mentioned no specimen in his original description of *A. ellipticum*, but did say that it occurred outside of Caracas, and that it was "brought to Europe by the famous Moritzi from Caracasan regions" (translated from Latin by Dan Nicolson, pers. comm.). It is unclear whether he was referring to a Moritzi collection, but it is likely that he had seen the May 1852 Gollmer collection that is here lectotypified, perhaps after its having been brought to his attention by Moritzi. In the third case, Schott described *A. rugosum* in 1858, citing no specimen. However, in 1860, in his *Prodromus*, he mentioned both a Gollmer and a Wagener collection; the Gollmer collection has here been accepted as the lectotype. In the fourth case Schott described *A. egregium* in 1860, again citing no specimen. His plate of drawing 482 deposited at W and represented by microfiche number 13A-7 in his *Icones Aroideae et Reliquiae*, serves as the lectotype of this species. Lastly, Schott cited no specimens in his original description of *A. fontanesii*, citing only that it was cultivated at Schönbrun. His illustration 496 serves as the type.

NETHERLANDS ANTILLES. CURAÇAO: 350 m, *Wilde 6A* (WAG). COLOMBIA. CÉSAR: Sierra Nevada de Santa Marta, SE slopes, Donahui, along trail to Chimencumena, 1,300 m, *Plowman & Davis 3699* (COL, GH); road from La Paz to Manaure, 460 m, *Cuadros & Gentry 3468* (MO), *3465* (MO), Guajira, Serranía La Macuira, SE edge of Cerro Huararech region, 550 m, *Sugden 63* (K); Cerro Manzano, 500–760 m, *Saravia 2424* (COL, US); Guasaira, 600–750 m, *Saravia & Saravia 3561* (COL, US); Palua, 650 m, *Sugden 216* (COL, FHO, K). MAGDALENA: Sierra de Pireja, E of Manaure, Hacienda Nuevo Horizonte, El Podrido, 1,550–1,600 m, *Cuatrecasas & Romero C. 25375* (US); Mpo. Santa Marta, Constante–Pueblito, 100–400 m, *Romero C. 8023* (COL). SANTANDER: Río Lebrija, NW of Bucaramanga, 400–700 m, *Killip & Smith 16298* (US). VENEZUELA. Cult. Berlin, *Engler 193* (GH). ARAGUA: vic. Cata, *Bunting 4493* (MO); 50 m, *Bunting 4355* (NY); Ocumare de la Costa–Cata, above Playa de Cata, *Bunting 2197* (MY), *2198* (NY), *2199*, *2200* (MY); Dtto. Girardot, Cata–Catica, 10–100 m, *Badillo 4904* (MY); Henri Pittier National Park, < 50 m, *Carnevali et al. 2329* (VEN); Ocumare–Turiamo, *Bunting & Holmquist 1978*, *1979* (NY); Maracay–Ocumare, 0.5–2 km NW of Rancho Grande, hillsides of Cordillera de la Costa, 1,200 m, *Bunting 2015* (NY); near Rancho Grande, 1,200 m, *Bunting 1966* (NY); Cerro La Mesa, 1,500–1,900 m, *Bunting 4721* (NY); La Cumbre de Rancho Grande trail, 1,200–1,300 m, 10°21′N, 67°39′W, *Bunting 3266* (MY), *Davidse et al. 16732* (VEN); Cata–Cuyagua, 8–9 km E of Cata, 400 m, 10°29′N, 68°42′W, *Bunting et al. 13501*, *13508*, *13509*, *13510*, *13511* (MO); Colonia Tovar–El Limón, *Bunting 2146* (NY). BOLÍVAR: Altiplanicie de Nuria, 500 m, *Bunting & Holmquist 4327*, *4328* (MY). CARABOBO: Puerto Cabello, *Preuss 1552* (B, BM), *Bunting 4353* (NY); Quizandal, *Trujillo 9581* (MY). DISTRITO FEDERAL: Caracas Higuerote, *Bunting 3275* (NY); Caracas–La Guaira, *Rose & Rose 21753* (US); 25 km E of La Guaira by air, 4 km E of Naiguatá on road to Los Caracas, 0–60 m, 10°38′N, 66°42′W, *Liesner & Steyermark 12324* (MO), *Bunting 2144-1* (MO); 2 km E of Los Caracas, *Bunting & Steyermark 2144-2*, *2144-3* (NY); Maiquetia, 40 m, *Andre 289* (K); Silla de Caracas, 1,300 m, *Elias 475* (F); Caracas Botanical Garden, 870–980 m, *Berry s.n.* (MO), *Braun 9* (VEN), *Croat 38338* (MO, PMA, SEL, US), *54412*, *54415* (MO), *54416* (CM, MO), *54418* (CM, F, MO); Cerro El Avila, Quebrada Chacaito, 1,600 m, *Manara s.n.* (VEN); Río Macarao, *Montes 74*, *279* (VEN); Río San Julian, just above Carrabelleda, 10–300 m, *Bunting 2050* (NY), *2050 N*, *2050 J* (NY). FALCÓN: Cerro Socopo, 1,200–1,560 m, 10°29′N, 70°48′W, *Liesner et al. 8356*, *8386* (MO, VEN); Parque Nacional Quebrada de la Cueva El Toro, trail to La Piedra, 600–900 m, 10°50′N, 69°7′W, *Liesner et al. 7864* (MO, VEN); Sierra de San Luís, Curimagua–San Luís, 1,300–1,400 m, *Steyermark 99149* (NY, US, VEN); Sierra de San Luís, Coro–Churumagua, 450 m, *Bunting 2844*, *2846* (NY); Dtto. Bolívar, El Puente, 340 m, *Ruiz et al. 481* (VEN); Dtto. Silva, Cerro Chichiriviche, above Soledad, 200 m, 10°51′N, 68°20′W, *Steyermark & Manara 110812* (MO, VEN); Dtto. Zamora, Cerro Mampostal, 400 m, 11°27′N, 69°17′W, *González 1068* (MO, VEN). LARA: Sanare–Yacambú, road through Parque Nacional Yacambú, 7.6 km past entrance, 1,500 m, 9°42′N, 69°36′W, *Croat 54698* (MO); Humocaro Alto–La Palma, 1.5 km S of La Mesa, 1,280 m, 9°35′N, 70°01′W, *Croat 60621* (CM, K, MO, RSA); Dtto. Jiménez, Alto del Viento–Cerro Pando, 1,000–1,700 m, 9°39–42′N, 69°34–36′W, *Davidse & González 21186* (MO); dirt road 17 km E of Duaca, 1,200 m, 10°17′N, 69°02′W, *Croat 60617* (AAU, MO, VEN); Dtto, Torres, Lara–Zulia, Agua Linda, ca. 35 km E of El Venado, 1,300 m, *Bunting & Fucci*

13475 (NY); 1,100–1,200 m, *Bunting & Stoddart 9753* (NY). MÉRIDA: Mérida–La Azulita, La Chorrera (waterfalls N of hwy.), between Las Cruces and La Calera, 8°35′N, 71°16′W, *Croat 54794* (MO); 28 km W of Mérida–El Vigia intersection, 1,120 m, *Bunting 2602, 2602J* (MY, NY); 9 km above Plaza Bolívar in La Azulita, SE of La Azulita, 1,590 m, 8°44′N, 71°26′W, *Croat 54856* (MO); Mérida–Lagunilla, ca. 2 km S of Mérida, near intersection with road to La Azulita, *Bunting 2740* (MY, NY); Mérida–El Vigia, 26 km above El Vigia, 850 m, *Bunting 2309B* (MY, NY); Caño Zancudo–La Azulita, border of Caño Blanco (Puente Hierro), *Bunting 4382* (MY); 6 km above Caño Zancudo, near bridge across Caño Ron (second bridge), *Bunting 2798* (MY); El Vigia–Tovar, Km 5, 3 km S of junction to Mesa Bolívar, 5 km N of Santa Cruz de Mora, 450 m, 8°26′N, 71°44′W, *Croat 54877* (B, MO); 5 km N of El Morro, 1,800 m, 8°25′N, 71°10′W, *Hahn & Grifo 3320* (MO); Montaña Salinas, Mesa Bolívar, 1,300–1,400 m, *Bernardi 633* (NY); Tovar de Mérida–Panamerican Hwy., 2 km above Zea, 975 m, *Bunting 2574* (NY). MIRANDA: Los Caracas–Higuerote, 1 km E of Osma, *Bunting 3298* (CM, MO, NY); Morros de la Guairita, 880–1,000 m, *Berry 1829, 1897* (VEN); Quebrada Garita headwaters, N of Mérida, Vista Linda, 1,000 m, 10°26′N, 66°49′W, *Steyermark & Berry 111961* (VEN). PORTUGUESA: 15 km E of Chabasquen, 67 km NNW of Guanare, 1,450–1,520 m, 9°26′N, 69°54′W, *Steyermark et al. 126795* (MO). TÁCHIRA: Lobatera–Urena, 13 km NE of Lobatera, near La Victoria, 3,650–3,750 ft., *Bunting 2352* (MY, NY); 1,216–1,250 m, *Bunting 2351, 2351 J* (MY, NY); Rubio–San Antonio, 11 km W of Rubio, *Bunting 11665* (NY); Rubio–Las Delicias, 2 km above Matamulas, 14 km N of Las Delicias, *Bunting 4397* (MY); 6 km above Las Delicias, 5,500 m, *Bunting 2313B* (MY), *Bunting 2313A* (NY); San Cristóbal–Santo Domingo del Táchira, Agua Dulce, *Bunting 2372* (MY); 10 km E of La Fundación, Represa Dorada, 600–1,000 m, *Liesner & González 10189, 10329* (VEN); 35 km SSE of San Cristóbal, La Buenana, 6–12 km W of Quebrada Colorado, 600–1,200 m, 7°28′N, 72°09′W, *Liesner & González 10865* (VEN); Pregonero–La Fundación, 19 km S of Pregonero, 1,200 m, 7°57′N, 71°45′W, *Croat 54948* (MO); San Cristóbal–Delicias, 45 km SW of San Cristóbal, 19 km N of Delicias, 1,300 m, 9°42′N, 72°25′W, *Croat 55031* (MO); San Cristóbal–Chorro del Indio–Caño Seco–La Florida, 1,100–1,200 m, *Bunting 11645* (NY); 1,100 m, *Bunting 13403* (NY); San Cristóbal–Cordero, San Rafael–Cordero, 900–1,000 m, *Bunting 4814* (NY); Maracay–Choroní, 19 km from Maracay, along S slope of northern cordillera, 1,280–1,300 m, 10°18′N, 67°24′W, *Croat 54499* (CAS, F, MO); La Fria, at Las Pavas, along Caño Aguas Calientes, 125–200 m, *Bunting 13390* (NY); La Grita–Pueblo Hondo, ca. 7–8 km N of La Grita, 1,600–1,700 m, *Bunting 11668* (NY); Dtto. Ayacucho, *Bunting & Chacón 4983* (MO, NY); Dtto. Junin, Villa Paez–Betania, 2,050–2,350 m, *Bunting 4958* (NY); Dtto. Cárdenas, above Palmira, 1,800 m, *Bunting 4847* (MO); Dtto. Cárdenas, on the outskirts of Cordero, 1140 m, *Bunting 4864* (NY); above Palmira on the outskirts of San Cristóbal, 1,800 m, *Bunting 13451, 13452* (NY); Dtto. Lobatera, La Cazadora, 1,600 m, 7°55′N, 72°18′W, *van der Werff & Ortiz 5614* (MO); 2,000 m, *van der Werff & Ortiz 5450* (MO). TRUJILLO: Agua Viva–Carora, 20 km NE of Agua Viva, E of Valerita, 150 m, *Bunting 2822* (MY). YARACUY: on road to Candelaria, 7.5–8 km N of Salom, NE of Nirgua, W of Valencia, 1,200 m, 10°11′N, 68°30′W, *Croat 54652* (MO, RSA); Cerro La Chapa, N of Nirgua, 1,200–1,360 m, *Steyermark & Bunting 97722* (VEN); on the outskirts of Aracal, ca. 7 km NW of San Felipe, 600–800 m, *Bunting 2003 S* (NY). ZULIA: Perijá, 1,175 m, *Gines 1926* (US); Serraniá de Perijá, Río Omira-kuna (Tumuriasa), near Colombian border, SE of Pishikakao and Iria, 1,470–1,560 m, *Steyermark et al. 91156* (MO, VEN); Hacienda Los Chorros, 600 m, *Ferrari & Trujillo 1535* (MY); Dtto. Mara, Puesto "El Bosque" de la Guardia Nacional, 1,450–1,600 m, 10°47′N, 72°40′W, *Bunting et al. 12068* (MO), *12227* (MO, NY); Dtto. Mara, river basin of Río Guasare, outskirts of Destacamento Guasare, 600–700 m, *Bunting et al. 12810* (NY); Cumbre de Rancho Grande trail, 1,200–1,300 m, 10°21′N, 67°39′W, *Bunting 3266* (MY).

Anthurium crenatum (L.) Kunth, Enum. Pl. 3: 75. 1841. *Pothos crenata* L., Sp. Pl. ed. 2: 1373. 1763. TYPE: Virgin Islands: St. Thomas, C. Plumier illustration published by J. Burman, Plant. Amer. Fasc. t. 39. 1756 serves as the type. Figures 106, 111, 115.

Anthurium acaule var. *portoricensis* Kuntze, O. Ktze. Rev. Gen. 2:738. 1891. TYPE: Puerto Rico, *Kuntze s.n.* (holotype, MO; isotype, K).

Anthurium acaule var. *brevipes* Engl., Bot. Jahrb. Syst. 25: 362. 1898. TYPE: Puerto Rico, *Sintenis 1582* (holotype, B; isotype, K).

Epiphytic or epilithic, sometimes forming dense clumps; stem to 9 cm long; roots moderately dense, spreading to descending, pale green pubescent, elongate, blunt, 3–4 mm diam.; cataphylls subcoriaceous, narrowly lanceolate, weakly 1-ribbed near apex, 9.5–13 cm long, narrowly acute at apex with a subapical apiculum, light green, drying reddish brown (B & K yellow 5/2.5), persisting semi-intact, eventually deciduous. *Leaves* erect to spreading; petioles 2.5–29.5 cm long, 4–17 mm diam., sharply to bluntly D-shaped, shallowly and broadly sulcate adaxially, the margins sharp but not raised, rounded to 3-ribbed abaxially, the surface weakly pale-speckled; geniculum slightly thicker and paler than petiole, 0.6–1.3 cm long; blades moderately coriaceous, broadly to narrowly oblanceolate or elliptic, sometimes ± oblong, acute to acuminate at apex (the acumen apiculate), acute (rarely weakly subcordate) at base, (18)23–100 cm long, 4–28 cm wide broadest near or above the middle, the margins sinuate to undulate; upper surface semiglossy, medium to dark green, lower surface weakly glossy to semiglossy, paler; midrib acutely angled at base, gradually becoming weakly sunken near the apex above, prominently higher than broad at base, becoming prominently convex toward the apex below, paler than surface; primary lateral veins 8–18 per side, departing midrib at

(30)40–75° angle, ± straight to arcuate-ascending to the margin, raised above, convexly raised below; tertiary veins weakly raised above and below, darker than surface, drying prominently raised; reticulate veins weakly visible above, prominulous and slightly darker than surface below, conspicuously raised when dried; collective vein arising in the upper ⅓ of the blade or absent, 5–12 mm from margin. *Inflorescences* erect to spreading or pendent; peduncle 19–72 cm long, 3–7 mm diam., 1.6–14.4× as long as petiole, green, terete to ellipsoid in cross section; spathe erect to spreading, subcoriaceous, sometimes flushed pink or maroon, usually light green (B & K yellow-green 7/10), linear-oblong, with the margins curled under, 4–14.5 cm long, 0.4–1.5 cm wide, acuminate at apex, obtuse to rounded at base; spadix reddish or purplish violet to maroon (dull, dark bluish purple fide S. Mayo, 1982), long-tapered, somewhat curved, 6.5–25 cm long, 3–8 mm diam. near base, 2.5–4 mm diam. near apex, broadest at the base; flowers scented like rotting fruit prior to anthesis, rhombic to square, 1.5–3 mm long, 1.6–2.2 mm wide, the sides prominently and smoothly sigmoid; 5–8 flowers visible in principal spiral, 8–12 in alternate spiral; tepals matte to weakly glossy, densely, minutely papillate; lateral tepals 0.6–1.4 mm wide, the inner margins straight to rounded, the outer margins 2-sided; pistils emergent 2–3.5 mm, glossy, green; stigma linear, 0.2–0.4 mm long, brushlike; stamens emerging in a slow, regular sequence from the base, the laterals preceding the alternates by 10 spirals; filaments translucent, broader than anthers, ca. 0.5 mm long; anthers 0.3–0.6 mm long, 0.5–0.8 mm wide; thecae oblong-ellipsoid to oblong-ovoid, weakly divaricate; pollen yellow-orange, fading to white (B & K yellow 8/5). *Infructescence* spreading-pendent; spathe withered, usually deciduous; spadix to 2.5 cm diam.; berries bright red (B & K red 4/5), obovoid, glossy, 8–10 mm long, 5–6 mm diam.; mesocarp mealy, white, sweet, becoming acrid; seeds tan to pale yellow, oblong-elliptic, 3.8–6 mm long, 2–2.8 mm wide, 1.5–1.8 mm thick, with a short gelatinous appendage at apex.

Anthurium crenatum is endemic to the northwestern part of the West Indies, where it is known from the Dominican Republic, Puerto Rico, and the small islands to the east of Puerto Rico, namely Vieques, Culebra, St. Thomas, St. John, Tortola, and St. Croix (all but Vieques are part of the U.S. Virgin Islands). It occurs principally in humid forests from near sea level to 900 m. "Dry evergreen woodland" is noted for *Mori & Woodbury 16999*, from St. John.

This species is characterized by its usually narrowly oblanceolate, short-petiolate blades which have conspicuously raised tertiary and reticulate venation on drying and sometimes even on live plants, and by its long-pedunculate inflorescence, which is usually pendent, with a long-tapered, dark purplish violet to maroon spadix and a promptly withering, linear-oblong spathe.

Anthurium crenatum is not easily confused with any other species and is the only member of sect. *Pachyneurium* in the areas where it occurs. It is perhaps most closely allied to *A. crassinervium* of northern South America and Curaçao.

Anthurium crenatum has been confused since Schott's time with *A. acaule* (Jacq.) Schott. See the discussion of the history of this taxonomic confusion by Mayo (1982), whose paper dealing with the West Indian bird's nest *Anthurium* species demonstrates that *A. acaule* is actually a completely different species endemic to Martinique and is probably a member of sect. *Urospadix*, with most of its relatives in Brazil. Howard (1979) erroneously associates the name *A. acaule* with *A. hookeri*.

BRITISH VIRGIN ISLANDS. TORTOLA. Dotys, *Fishlock 368* (GH, K); High Bush, 375 m, *Britton & Shafer 811* (NY, US). DOMINICAN REPUBLIC. Parque Nacional Los Haitises, Monte Plata, 250 m, *Garcia et al. 664* (NY); Liali, 100–500 m, *Abbott 2601* (US); Miches–El Seibo, at crest of Cordillera Oriental, 600 m, *Gastony et al. 694* (GH, NY, US); Río Comatillo, Bayaguana, 150 m, *Liogier 22465* (JBSD); Río San Juan, *Miller 1125* (US); Sabana del Mar, 100 m, *Liogier 18507* (NY, US). LA ALTAGRACIA: 21 km W of hwy., 200–350 m, *Pimentel 83* (JBSD, NY); "El Caracol" (where old road parallels Río Dueye), N of Boca de Yuma, 18°24′N, 68°37′W, *Zanoni et al. 10685* (JBSD); La Colorada, near headwaters of Río Llano, Km 22 on road from Santana to La Colorada, NW of hwy., 18°46′N, 68°44′W, *Mejia & Ramirez 11133* (JBSD, MO, USD); Hato de Mana, Dueye, Río Dueye, 10 km N of Hato de Mana, trail toward Las Auyamas, 18°45′N, 68°50′W, 100 m, *Mejia & Ramirez 11229* (JBSD); 21 km W of Higuey, road to El Seibo, Loma del Penon, 200–350 m, *Zanoni & Mejia 17332* (JBSD); 0.5 km from Otrabanda on road from Cruce de Los Islenos and Nisbon at Arroyo Yaoya, 18°39′N, 69°39′W, *Zanoni et al. 18967XX* (JBSD). SAMANÁ: 9 km NE of Samaná, rd. to La Laguna, and Loma Pan de Azucar, 50 m, 19°15′N, 69°16′W, *Gentry & Zanoni 50600* (MO); Loma Pan de Azucar, E of La Laguna, NE of Santa Barbara de Samaná, 19°15.5′N, 69°18′W, 100 m, *Zanoni & Gentry 34116* (JBSD); Peninsula de Samaná, Loma El Fronton, 19°17′N, 69°10′W, 100–256 m, *Zanoni et al. 29346* (JBSD, MO, NY, USD); Sanchez, *Rose et al. 4396* (NY, US), *Wright et al. 536* (GH, US); Las Canitas Mts., 330 m, *Taylor 7* (GH, US); 3.5 km E of Las Terrenas, 5 km S of Callejon, 19°18′N, 69°30′W, *Zanoni & Mejia 17634* (JBSD). SAN CRISTÓBAL: 8.5 km from Comatillo on road to Cruce de Pilancon and Pilancon, 18°52′N, 69°37′W, *Zanoni & Mejia 16411* (JBSD); Río Capita (de Trinidad), 15 km from Comatillo on road to Sierra de Agua and Trinidad Mejia, 18°50′N, 69°34′W, *Zanoni & Mejia 16318* (JBSD, MO, USD). SIEBO: Cordillera Oriental, along rock road

9.2 km SE of Miches, along Río Yeguada Arroyo Santiago, 100 m, 18°55′N, 69°9′W, *Croat 68550* (MO); Arroyo Las Cabirmas, 5 km S of Miches–Nisibon Hwy., on road to Las Cabirmas, 18°55′N, 69°01′W, 100 m, *Zanoni et al. 15946* (JBSD); El Salado–Otrabanda, Higuey, *Ekman 12243* (GH, K, US); Hato Mayor del Rey, 400–500 m, *Allard 13632* (US); Hato Mayor–Sabana del Mar, Guamira, *Jimenez et al. 4129* (NY); Hato Mayor del Rey, 18°49.5′N, 69°19′W, *Zanoni et al. 11966X* (JBSD); Higuey, *Howard & Howard 9790* (BM, GH, NY, US); 11.7 km W of El Valle, trail to Trepadora Alta, 18°58′N, 69°28′W, *Zanoni et al. 21283* (JBSD). HAWAII. Oahu, cultivated at Foster Gardens, Wahiawa, *Croat 45013* (MO), *45016* (B, MO). PUERTO RICO. Adjuntas, Las Cruces, *Sintenis 4205* (MO, NY, P); Arecibo–Utuado, *Britton & Cowell 345* (NY, US), *Eggers 1142* (P), *Underwood & Griggs 846* (NY, US); Bayamon, *Arsene et al. s.n.* (B, NY), *Stevenson 384* (US), *Underwood & Griggs 908* (NY, US); Bayamon, Finca Sánchez, *Hioram s.n.* (NY, P); Finca Nevares, 50 m, *Acevedo & Chinea 2143* (NY); Hato Tejas, 50–100 m, *Webster & Miller 8607* (US); Candelaria, *Goll et al. 279* (NY, US); W of Candelaria, Km 21.5 on Route 2, 80 m, 18°24′N, 66°14′W, *Solomon 5762* (MO, SEL); Cayey–Guayama, *Underwood & Griggs 336* (NY, US); Coamo Springs, *Britton et al. 5971* (NY); Coco Beach, 18°22′N, 65°48′W, *Boom 8013* (NY); Guayama Road, Quebrada Arriba, *Goll et al. 632* (US); Juana Díaz, Peñas de las Cuevas, *Britton & Marble 2296* (NY, US); Laguna Tortuguero, *Wagner 286* (U); 2 mi. N of Mameyes, 50 m, *Hartley 13373* (U, US); Maricao, *Sintenis 479* (BM, GH, K, US); Mayagüez, *Heller 6283* (E, GH, MO, NY, P, US); Morovis, 300 m, *Liogier 30065* (MO); Palmer–Florida Road, *Wagner 203* (GH); San Juan, *Hioram* (Rose) 7 (11.298) (NY, US), *Hornbeck s.n.* (W), *Krebs s.n.* (C, W), *Kuntze s.n.* (K, NY), *Riedel s.n.* (P); San Narciso, *Britton & Britton 7270* (NY); Santurce, *Heller & Heller 1267* (NY, US); Utuado, *Britton 5224* (NY); Yauco, *Garber 104* (GH, K, NY); Dorado Beach Forest, Dorado, Dorado Beach Hotel, 10 m, *Croat 60851* (B, CM, MO, RSA); El Dorado forest, N coast, 18°28′N, 60°16′W, *Luteyn & Luteyn 11466* (NY); Río Abajo State Forest, Hwy. 621, near end of asphalt road, 360–390 m, 18°19′N, 66°40′W, *Croat 60860* (MO, US); Río Piedras, *Johnston 151, 901* (NY); Sierra de Luquillo, Mt. Jimenes, *Sintenis 1582* (K); Sierra de Naguabo, 210–675 m, *Shafer 3392* (NY). CULEBRA: *Britton & Wheeler 114* (NY, US). MANATÍ: 2 mi. NE of Manatí, *Hansen et al. 9068* (MO, USF). VIEQUES: *Eggers s.n.* (GH), *Grosgourdy 13* (P); Isabel Segunda–Capo Cielo, *Shafer 2377* (NY, US). U.S. VIRGIN ISLANDS ST. JOHN: Bethania–Rosenberg, *Britton & Shafer 225* (NY, US); Bordeaux, 330 m, *Britton & Shafer 545* (NY, US). ST. THOMAS: Bourne Resolution, *Britton & Marble 428* (NY); above Cinnamon Bay, road to Herman Farm, 60–120 m, *Mori & Woodbury 16999* (MO); Pearl–Bourne Resolution, *Britton & Marble 1320* (NY, US), *Eggers 307* (GH, NY), *Friedrichsthal s.n.* (K, W), *Krebs s.n.* (K, W), *s.n.* (NY), *Raunkiaer s.n.* (P, US), *Richard s.n.* (P); Signal Hill, 500 m, *Eggers 308* (K, P), *475* (US), *814* (P), *Eggers s.n.* (Engl. Arac. no. 191) (GH, K, P, US).

Anthurium cubense Engl., Bot. Jahrb. Syst. 25: 364. 1898. TYPE: Cuba. Monte Toro, 300 m, *Eggers 5402* (holotype, B; isotype, K). Figures 1, 112, 113, 116, 117.

Epiphytic or terrestrial; stem short, to 3 cm diam.; roots dense, ascending, green when young, becoming gray, pubescent at base, becoming smooth, tapered or ending abruptly, ca. 5–10 cm long, 3–5(8) mm diam.; cataphylls subcoriaceous, lanceolate, (4)10–22 cm long, narrowly acuminate at apex, drying reddish brown (B & K yellow-red 4/10), persisting ± intact, weathering into coarse linear fibers and persisting around stem. *Leaves* erect; petioles (4)6–16(36) cm long, (2)5–12 mm diam., C-shaped to D-shaped, broadly sulcate adaxially, rounded to obscurely flattened abaxially; geniculum slightly thicker than petiole, 0.5–1.5 cm long; sheath (1)3–8 cm long; blades subcoriaceous, usually oblanceolate-elliptic, sometimes ± elliptic, short to long-acuminate at apex, usually obtuse at base, sometimes acute or weakly rounded, (20)33–95 cm long, (5.5)13–38 cm wide, broadest at or near the middle, the margins conspicuously undulate; upper surface semiglossy, medium green (B & K green 5/2.5), lower surface matte, slightly paler, both drying grayish; midrib flat to convexly raised at base, becoming obtusely raised toward the apex above, broadly angular to 3-ribbed below; primary lateral veins 6–11 per side, departing midrib at 30–50° angle, ± straight to the margin, convexly raised above and below, slightly paler than surface; tertiary veins obscure, weakly raised to prominulous when dried; reticulate veins visible, darker than surface, obscure when dried; collective vein arising in the upper ⅓ to upper ¼ of the blade or absent, equally as prominent as primary lateral veins when present. *Inflorescences* erect, rarely spreading, usually several at different stages of development per plant; peduncle (5.5)8–33 cm long, (2)5–10 mm diam., 0.4–1.2× as long as petiole, green tinged violet, terete; spathe reflexed at anthesis, rarely recurled, subcoriaceous, green tinged with violet-purple, ovate to lanceolate, (2.5)5–16 cm long, (0.6)1–5 cm wide, broadest near the base, acute to acuminate at apex, rounded at base; stipe to 2 cm long in front, to 1 cm long in back; spadix purplish (B & K purple 4/5) to pale violet-purple (B & K purple 6/7.5), cylindroid, slightly tapered toward both ends, (2.5)8–19 cm long, (4)6–10 mm diam. near base, (3)5–9 mm diam. near apex; flowers rhombic to 4-lobed, (1.3)2.1–2.6 mm long, (1.7)2–2.6 mm wide, the sides weakly sigmoid, sometimes straight; 9–12 flowers visible in principal spiral, (9)14–16 in alternate spiral; tepals matte, pale punctate, slightly roughened; lateral tepals 0.7–1.4 mm wide, the inner margins straight to weakly convex, the outer margins 2-sided; pistils weakly raised, greenish, darker than tepals; stigma linear, 0.4 mm long; stamens emerging in a scattered pattern through-

out the spadix, laterals emerging almost to apex before alternate emerge, held just above tepals and against pistil, obscuring the latter at anthesis; anthers white tinged with red-violet; thecae oblong, not divaricate; pollen white. *Infructescence* spreading or erect; spathe persisting, brown; spadix ca. 14–27 cm long, 2–2.5 cm diam. (not including exserted berries), with the berries scattered throughout; berries orange-red (B & K yellow-red 5/2.5), ellipsoid, subtruncate and subapiculate at apex, 9–14 mm long, 4.5–6 mm diam.; mesocarp juicy; usually 1, sometimes 2 seeds per berry, yellow (B & K yellow 9/5), oblong to ellipsoid, 5–7 mm long, 3–3.4 mm diam., with a gelatinous, sticky, transparent appendage.

Anthurium cubense is found in Cuba and drier parts of eastern Guatemala and Yucatan on the Atlantic slope, and in Nicaragua, Costa Rica, and Panama on the Pacific slope. In South America, it extends along the Caribbean coast from western Venezuela to Colombia, with one outlying collection known from the Río Patia in southern Colombia. It occurs in tropical dry forest, drier parts of tropical moist forest, and premontane wet forest from sea level to 700 m. It is most common in Cuba and Nicaragua.

This species is recognized by its short petioles, short inflorescences (much shorter than the leaves), its stubby, purplish to pale violet-purple spadix that is tapered toward the apex (or sometimes toward both ends), and by its bright red berries. It has no apparent close relatives and is not easily confused with any other species.

Engler (1905) also recognized material of this species under the name *Anthurium recusatum* Schott from Cuba. That name, however, has been misapplied and is probably synonymous with *A. fendleri* from South America. *Anthurium fendleri* is not closely related to *A. cubense*, though it has a similar rosulate habit. It differs chiefly in having a long-pedunculate inflorescence, narrowly tapered spadix, promptly withering spathe, and purple berries.

COLOMBIA. Isla de Providencia, Smooth Water Road, *Torres-Romero 295* (COL). ATLÁNTICO: Barranquilla, *Elis 1295* (F, US), *1404* (F). BOLÍVAR: Turbaco, Torrecilla, *Killip & Smith 14656* (GH, NY, US); Mpo. San Juan Nepomuceno, Santuario Nacional de los Colorados, 230–250 m, 9°58′N, 75°10′W, *Cuadros & Keating 60679* (MO). MAGDALENA: Dibulla, *Seifriz 263* (US); Santa Marta, *Smith 2763* (GH, K, NY); Quebrada El Cedro, 350–400 m, *Moreno 415* (COL). COSTA RICA. GUANACASTE: 5 km S of Peñas Blancas, 15 km N of La Cruz, 1.5 km E of main road, 0–300 m, 11°11′N, 85°37′W, *Liesner 4652* (MO). PUNTARENAS: Cabo Blanco Nature Reserve, *Burger & Liesner 6627* (F, MO). CUBA: without locality, *Sagra s.n.* (P); Finca Olimpo, *Hioram 3937* (US); Managua, *Baker 316* (NY, US); Matanzas, *Meisner s.n.* (NY); Monte Toro, 400 m, *Eggers 5402* (B, K), *Wright 3208* (BM, GH, K); Orientali, *Wright 601* (GH, K); San Diego de los Baños, *Britton et al. 6854* (NY), *León 4233* (NY, P). LA HABANA: La Guácima, *Abarca & O'Donovan 4688* (GH, NY); San Antonio, *Hitchcock s.n.* (F), *Van Hermann 822* (F, NY); Vento, *Curtiss 647* (BM, F, GH, K, MO, NY, P). LAS VILLAS: Hanabanilla Falls, *Britton et al. 4838* (NY); Santa Clara, *Rowe 8643* (GH), 8644 (NY). MATANZAS: Matanzas, *Britton & Shafer 377* (NY). ORIENTE: Bayate, *Ekman 6202* (NY); Firmeza-Gran Piedra, *Shafer 8936* (GH, K, NY); Paso Estancia, *Shafer 1573* (NY); San Luis, *Britton 2324* (NY); Rio Guama, upper part, 300 m, *Taylor 195* (NY). PINAR DEL RÍO: El Guama, *Palmer & Riley 317* (US); Río Mestanza, *Britton et al. 10152* (US, NY); Sierra de Anafe, *Britton et al. 9608* (NY), *Wilson 11492* (NY, US); Sierra Guayaba, *Shafer 13851* (A, NY); Mpo. Vinales, Sierra del Infierno, across Hwy. from Granja "Moncada," 18°14′N, 68°39′W, 150 m, *Proctor et al. 39314* (JBSD); Pasco Real, *Van Hermann 988* (GH). SANTIAGO: El Cobre, *Pollard & Palmer 389* (GH, MO, NY, US, F). GUATEMALA. ALTA VERAPAZ: Cubilgüitz, *Tuerckheim 8606* (US). GUYANA: Demerara, cultivated at Glasgow Bot. Gard., *Hooker s.n.* (K). NICARAGUA. BOACO: Boaquito–Sta. Lucia, 4 km E of Boaca, Hacienda Peñas Blancas, 400–600 m, *Grijaiva & Soza 4197* (MO, SAR). CHONTALES: *Vincelli 86, 87* (MO); Acoyapa–Río Oyate, 0.4 km SE of bridge over Quebrada Niscale, 50 m, 11°47′N, 85°01′W, *Henrich & Stevens 161* (MO); 1.9 km S of La Libertad, 530 m, 12°12′N, 85°10′W, *Stevens & Montiel 17513* (MO); 5.3 km W of Puente Lovago, Km 160.1, 150–170 m, 12°00′N, 85°12′W, *Stevens & Henrich 20524* (MO); 1.5 km E of San Pedro de Lovago, 260–280 m, 12°07′N, 85°07′W, *Moreno 16047* (MO); 2 km S of Acoyapa, *Nichols 1723, 1725* (MO); 2 km N of Santo Tomás, rd. to San Domingo, 340–380 m, 12°04′N, 85°06′W, *Moreno 16208* (MO); 2.8 km N of Cuapa, 400–500 m, 12°17′N, 85°23′W, *Pipoly 1571* (CAS); N of Cuapa, *Stevens 3662, 6107* (MO); Río El Bizcocho, Juigalpa–La Libertad, 17.4 km NE of Río Mayales, 350–400 m, 12°12′N, 85°17′W, *Stevens 4030* (MO); Río Oyate, Acoyapa–Morrito, 50 m, 11°44′N, 84°59′W, *Stevens 21631* (MO). ESTELÍ: Kukamonga, km 167, Belén, 660–800 m, 13°15′N, 86°21′W, *Moreno 21822* (MO). GRANADA: road to Cutirre, 10–13 km NE of Granada, 350–400 m, 11°50′N, 86°56–57′W, *Moreno 1471, 1516* (MO); Granada, 40 m, *Levy 88* (P); Isla Zapatera, NE of Hacienda El Cerro, 400–525 m, 11°40′40″N, 85°45′45″W, *Grijalva 1936* (MO); Isletas de Granada, Isla El Carraco, 35 m, *Martínez & Rivière 1543* (MO, MEX); Volcán Mombacho, *Neill 2730* (cult. at Kew) (B, K, M, MBM, MO, PMA, US); NE side, *Atwood & Neill AN82* (MO); 10 km S of Granada, finca "Las Delicias," 340–360 m, 11°51°N, 85°57′W, *Moreno & Henrich 8447* (MO); Finca Cutirre, 300–400 m, 11°59′N, 85°55′W, *Guzmán & Castro 2152* (MO); S of Hacienda Cutirre, 300–400 m, 11°49′N, 85°55′W, *Moreno 16442* (MO); Las Delicias–Hda. Cutirre, 400–500 m, 11°50′N, 85°56′W, *Moreno 16478* (MO); las Fincas María Auxiliadora–El Cacao, 400–500 m, 11°51′N, 85°56′W, *Moreno 442* (MO). MANAGUA: Managua, *Maxon et al. 7538* (US); Managua, cultivated, *Araquistain 398* (MO); Centro de Managua, cult. in garden at Sears dept. store, 120 m, *Araquistain 40* (L, MO). MASAYA: Volcán Masaya National Park, *Stevens 4444* (B, MO). RÍO SAN JUAN: San

Carlos, *Atwood 2028* (MO); W of San Carlos, 30–35 m, 11°08′N, 84°47′W, *Sandino 1773* (MO). RIVAS: Isla de Ometepe, Volcán Concepción, Altagracia "La Sabana," 200–500 m, 11°32′N, 85°35′W, *Robleto 133* (MO); N side of Volcán Concepción, 300–1,000 m, 11°33′N, 85°37′W, *Moreno 19827* (MO); NE of Volcán Concepción, 140–160 m, 11°33′N, 85°35′W, *Sandino 4240* (MO); Volcán Maderas, Mérida, vic. "Las Abejas," 500–700 m, 11°26′N, 85°32′W, *Robleto 293* (MO); NE side of Volcán Maderas, 600–900 m, 11°27′N, 85°29′W, *Moreno 19580, 19600B* (MO); Volcán Masearas, Santa Cruz, *Stevens 6626* (MO). ZELAYA: Caño Majagua, *Stevens 6894* (MO). PANAMA: CHIRIQUÍ: 1 km E of Remedios, 8°14′N, 81°50′W, *Nee 10104* (MO, PMA); Río Estí, Gualaca–Fortuna, 0.6 km E of Gualaca, 700 m, *Croat 48793* (FTG, MO). VENEZUELA: FALCÓN: Dtto. Silva, Golfete de Guare, "La Penita," S of Chichiriviche, 10–100 m, 10°54′N, 68°16–17′W, *Steyermark & Manara 110434* (MO). ZULIA: Quebrada Perayra, SE of Machiques, *Steyermark 99847* (MY); Serranía de Perijá, Río Palmar, *Chitty & Benkowski 3061* (VEN); SE of Machiques, *Steyermark & Fernandez 99638* (K, MY, NY, US); headwaters of Río Guasare, 280 m, *Gentry 41141* (B, MO); 6 km W of main road and 2 km S of Río Catatumbo, 20–100 m, 9°06′N, 72°142′W, *Liesner & Gonzalez 13274* (MO); Dtto. Colón, Laguna de Congo, *Lescarboura 55* (MY); Dtto. Mara, El Palmar, *Medina 902* (MY); Caño Indio, Hacienda Caño Azul–Base of Cerro Yolanda, *Steyermark et al. 122640* (VEN); Cerro Negro, SE of Río Guasare, *Steyermark et al. 122687, 122690* (MO, VEN); Río Socuy, W of Cerro Caracara, SW of Corpozulia Campamento Socuy, *Steyermark et al. 123115* (VEN); Dtto. Perijá, La Villa de Rosario, foot of Sierra de Perijá (via Arimpia), 20–25 km W of La Villa, 225–350 m, *Bunting et al. 8800* (MO, NY); Quebrada Cosira, SW of Los Angeles de Tucuco, *Davidse et al. 18531* (MO, VEN).

Anthurium curtispadix Croat, sp. nov. TYPE: Ecuador. Pastaza: Puyo; originally collected by Mickey Carmichael, *Croat 55207* (holotype, MO 3104658; isotypes, AAU, B, K, M, NY, RSA, U, US; cult. at MO). Figures 114, 118, 123.

Caulis ad 21 cm longus, 3 cm diam.; cataphyllum persistens semi-intactum; petiolus 3.5–14 cm longus, 4–9 mm diam., D-formatus ad C-formatus, adaxialiter sulcatus; lamina elliptica ad oblanceolata, 17–57 cm longa, 7.5–20 cm lata; nervis primariis lateralis 5–7 utroque. Pedunculus 5–10 cm longus, 4 mm diam., effusus; spatha pallida viridis, oblongo-lanceolata, 3–3.5 cm longa, 1.5–2 cm lata; spadix erectus, cylindricus, 3.5–4.7 cm longus, 6–7 mm diam., pallide viridis. Baccae ignotae.

Stem to 21 cm long, ca. 3 cm diam.; leaf scars conspicuous or obscured by root mass, 0.5–1 cm high, 0.6–0.8 cm wide; roots ascending to spreading to descending, green to light brown (B & K yellow-red 9/7.5), smooth to sometimes weakly pubescent, tapered, elongate, 4–7 mm diam.; cataphylls subcoriaceous, weakly 1-ribbed near the apex, 5–8 cm long, narrowly acute and apiculate at apex, drying tan to reddish brown, persisting semi-intact, eventually as a reticulum of fibers with the apex remaining intact. *Leaves* erect to spreading; petioles 3.5–14 cm long, 4–9 mm diam., D-shaped to C-shaped, slightly sulcate adaxially, with the margins sharply to obtusely raised, rounded to sometimes obscurely 1–2-ribbed abaxially, the surface obscurely short-lineate; geniculum paler and thicker than petiole, becoming minutely and transversely fissured and scurfy abaxially, (0.7)1–2.2 cm long; blades subcoriaceous, elliptic to oblanceolate, gradually acuminate at apex (the acumen apiculate), narrowly acute to obtuse to weakly rounded at base, 17–57 cm long, 7.5–20 cm wide, broadest at or above the middle, the margins weakly undulate; upper surface semiglossy, medium green, lower surface matte to weakly glossy, paler, drying greenish to yellowish green; midrib flat at base with blunt medial rib, narrowing and acute toward the apex above, convexly raised and paler than surface below; primary lateral veins 5–7 per side, departing midrib at 30–45° angle, ± straight, raised and weakly paler than surface above, convex below; interprimary veins absent; tertiary veins obscure above, visible below; reticulate veins obscure above, darker than surface below; collective vein arising from near the apex, weakly sunken above, prominulous below, 2–9 mm from margin. *Inflorescences* spreading, usually several present at once; peduncle 5–10 cm long, 4 mm diam., equaling to usually ca. 0.5× as long as petioles, green (B & K yellow-green 6/7.5), terete; spathe reflexed-spreading, coriaceous, pale green, sometimes weakly tinged with red (B & K yellow-green 8/10), oblong-lanceolate, 3–3.5 cm long, 1.5–2 cm wide, broadest in the lower ⅓, inserted at 75° angle on peduncle, gradually to abruptly acuminate at apex (the acumen inrolled, hooked), acute to decurrent at base, the margins strongly downturned, meeting at 60–80° angle; spadix pale, dull green, somewhat tinged with brown, sessile, cylindroid to sometimes weakly clavate, erect, held at ca. 90° angle from peduncle, 3.5–4.7 cm long, 6–7 mm diam. near base, 3–4 mm diam. near apex, broadest at the base; flowers rhombic to 4-lobed, 1.7–2.3(2.6) mm long, 1.3–2.3 mm wide, the sides straight to jaggedly sigmoid; 13–15 flowers visible in principal spiral, 9 in alternate spiral; tepals matte, minutely papillate; lateral tepals 1.5–1.8 mm wide, the inner margins broadly rounded, the outer margins irregularly 3-sided; pistils weakly emergent, purplish violet; stigma linear, slitlike, 0.3 mm long; stamens emerging in a prompt, erratic sequence, the laterals extending to the apex in a scattered pattern before the 3rd stamen emerges, laterals followed by alternates in a rapid succession but very irregularly

on the spadix (sometimes the 4th stamen appearing first); anthers white, 0.6 mm long, 0.7 mm wide, obscuring pistil; thecae ellipsoid, not divaricate; pollen drying white. *Infructescence* not seen.

Anthurium curtispadix is known only from a living collection made near Puyo in Pastaza Department, Ecuador, by Mickey Carmichael. It was probably collected in an area of premontane wet forest at ca. 1,000 m.

This species is distinguished by its short, spreading inflorescence with an erect, short, stubby spadix (hence the name) with many (9–15) flowers per spiral. It is probably most closely related to *A. ernestii*, which differs in having an erect inflorescence and cataphylls persisting as an intact network of fine, pale fibers.

ECUADOR. PASTAZA: Puyo, cult. at MO and originally collected by Mickey Carmichael, ca. 1,000 m, *Croat 55207* (AAU, B, K, M, MO, NY, RSA, U, US).

Anthurium dombeyanum Brongn. ex Schott, Prodr. 477–478. 1860. TYPE: Peru, without exact locality, *Dombey s.n.* (holotype, P). Figures 11, 13, 119–122, 127.

Anthurium cymatophyllum K. Koch & Sello in K. Koch, 1221 xi. 276. 1868. TYPE: destroyed, locality unknown, of cultivated origin said to be from Brazil (a tracing at Kew prepared by Masters from Koch's type specimen in Berlin serves as the type).

Anthurium agoyanense Sodiro, Anales Univ. Centr. Ecuador 19: 286. 1905. TYPE: Ecuador. Tungurahua: Agoyán waterfalls in Río Pastaza, slopes of Volcán Tungurahua, 1,550 m, *Sodiro s.n.* (holotype, B)

Anthurium agoyanense var. *eleutheroneuron* Sodiro, Anales Univ. Centr. Ecuador 19: 287, 1905. TYPE: Ecuador, Tungurahua: slopes of Volcán Tungurahua, vic. Machay, *Sodiro s.n.* (holotype, B).

Anthurium rigidissimum Engl., Pflanzenr. IV. 23B(Heft 21): 292. 1905. TYPE: Peru. Junín: Tarma, above Huacapistana, 1,900–2,000 m, *Weberbauer 2007* (holotype, B).

Anthurium rigidissimum var. *mutatum* Engl., Pflanzenr. IV. 23B(Heft 21); 292. 1905. TYPE: Peru. Junín: Tarma, above Huacapistana, 1,900–2,000 m, *Weberbauer 2158* (holotype, B).

Terrestrial or epilithic, rarely epiphytic; stem 20–30 cm long, 2–6 cm diam.; roots dense (the root mass to 20 cm wide), greenish to pale reddish, grayish when dried, sometimes with raphide cells on the surface, elongate, blunt at apex, to 40 cm long, 4–10 mm diam.; cataphylls subcoriaceous, lanceolate, 5–25 cm long, narrowly rounded to bluntly acute at apex, pale green, drying brown, persisting semi-intact at upper nodes, otherwise as coarse linear fibers, sometimes with the apex remaining intact. *Leaves* erect to spreading; petioles (3)10–30 cm long, 5–18 mm diam., erect to spreading, D-shaped, slightly thicker than broad in juveniles and lacking the medial rib adaxially, sulcate in age with an obtuse to acute medial rib, rounded (rarely 1–2-ribbed) abaxially, the surface pale-speckled; geniculum slightly thicker and paler than petiole, 0.5–2.5 cm long; sheath 3–11 cm long, extending halfway or throughout the petiole in smaller leaves; blades subcoriaceous to thickly coriaceous, oblong-lanceolate to oblanceolate or narrowly obovate, often elliptic in smaller leaves, bluntly acute or acuminate at apex (the acumen minutely apiculate), long-attenuate to obtusely rounded or subcordate at base, (10)40–190 cm long, (2)10–35 cm wide, broadest above or near the middle, the margins flat in smaller leaves or markedly undulate especially in larger leaves; upper surface glossy to semiglossy, dark to medium green, occasionally developing a bluish, glaucous covering with age, lower surface usually semiglossy, rarely matte, concolorous or paler than upper surface; midrib above acutely raised, below obtusely ribbed at base, becoming acutely angled in upper ⅓, and then convexly rounded toward the apex, paler than surface or concolorous with it; basal veins usually present and aggregated in subcordate leaves, arcuate-ascending, free to base; primary lateral veins (7)10–20(24) per side, departing midrib at (18)40–60(70)° angle, usually gently arcuate-ascending to within 1 cm of the margin, then abruptly ascending to the margin, convexly raised above; tertiary veins scarcely visible above, moderately to distinctly visible below, sometimes darker than surface, very weakly raised below or flat, drying raised and conspicuously visible; collective vein arising from near the base to near the apex, less prominent than primary lateral veins, sunken to weakly raised above, raised below, 2–10 mm from margin. *Inflorescences* erect-spreading to spreading-arching, shorter than or almost equaling leaves; peduncle (15)30–65(90) cm long, 2–11 mm diam., (2)3–7(10)× as long as petiole, pale green, sometimes tinged with red-violet, green to dark brown when dried, subterete, sometimes 1-ribbed, flexible; spathe spreading to reflexed at anthesis, recurled, subcoriaceous to coriaceous, green, sometimes tinged with red-violet, speckled with raphide cells, linear-lanceolate, 7–20 cm long, 1–3.5 cm wide, broadest near base, acute at apex, decurrent at base; spadix olive-green to grayish, becoming dark pink or maroon (B & K red-purple 2/2.5) to purplish at anthesis (B & K blue-purple 4/10), weakly to moderately tapered, rarely cylindroid, sessile to stipitate to 2.5 cm, ± erect, rigid, held at 130–180° angle from peduncle, 4–28 cm long, 4–17 mm diam. near

base, 3–11 mm diam. near apex, broadest near the base; flowers squarish to 4-lobed, to 3 mm long when fresh, 1.6–2.6 mm long when dried, to 2.5 mm wide when fresh, 1.4–2.2 mm wide when dried, the sides ± straight to smoothly sigmoid; 4–14 flowers visible in principal spiral, 3–8 in alternate spiral; tepals matte; lateral tepals 1–1.6 mm wide, the inner margins tinged with pink, becoming purplish, broadly convex, the outer margins 2–4-sided; pistils scarcely emergent, green, with raphide cells; stigma oblong, slitlike, 0.4–0.6(1.0) mm long; stamens emerging irregularly from the base of the spadix in a scattered pattern, slightly exserted, lateral stamens emerging to midway, the laterals preceding the alternates by 5–18 spirals, inclined over and obscuring pistil; filaments tan, with raphide cells, exserted ca. 0.5 mm, 1–2 mm long, 0.6–0.9 mm wide; anthers pinkish, 0.6–1.1 mm long, 0.5–1 mm wide, inclined over the pistil; thecae obovoid, scarcely or not divaricate; pollen pale orange to pale yellow fading to cream, yeasty scented. *Infructescence* semi-erect; spathe persisting; spadix 5–27 cm long, 1.5–2.5 cm diam., with berries scattered throughout; berries violet-purple to reddish violet (B & K purple 3/10), obovoid, bluntly rounded at apex, 6–8 mm long, 5–6 mm diam.; pericarp with raphide cells; mesocarp pulpy, white; seeds 1–2 per berry, green, oblong, 3.5–8 mm long, 2.5 mm diam., with a gelatinous appendage at apex.

Anthurium dombeyanum is an Andean species ranging from central Ecuador to southern Peru at 950 to 2,760 m. Collections from Ecuador are from the provinces of Tungurahua and Loja (a somewhat aberrant collection is known from Morona–Santiago; see below), while Peruvian collections are represented from Amazonas and Cajamarca to San Martín, Huánuco, Pasco, Junín, and Cuzco. Specimens from Ecuador ostensibly occur in lower montane moist forest to premontane moist forest life zones. In Peru, the species is present in lower montane and montane moist forest and premontane dry forest. The species occurs in seasonally dry habitats and often inhabits rocky or extremely precipitous sites, with low nighttime temperatures.

This species is recognized by its short-petiolate, coriaceous, usually markedly undulate blades, its long-pedunculate inflorescence with a moderately short-tapered, usually purple spadix, thick, green, lanceolate reflexed spathe and minutely papillate tepals with a more or less erose inner margin. Another feature common to most plants, despite their markedly variable blades (ranging from narrowly obovate to oblong-oblanceolate) is the primary lateral veins, which frequently extend nearly to the margin in an almost straight line before turning markedly upward and extending along the margin and gradually merging with it.

The only species which might be confused with *A. dombeyanum* is *A. leonianum*, from northern Ecuador, but only two collections of *A. dombeyanum* are known from anywhere near this area and fall short of reaching the same province (Imbabura). *Anthurium leonianum* is most easily distinguished by its petioles, which are 5–8-ribbed, rather than rounded abaxially. See that species for further discussion.

Anthurium cymatophyllum is doubtfully placed here in synonymy. Typical material is no longer existent, and the species is represented by a tracing of the type done by Masters and deposited at Kew and by a photograph taken before the type was destroyed in World War II. The species was described from a plant of cultivated but unknown origin. There was speculation it originated in Brazil, but it is almost certainly not of Brazilian origin. It most clearly fits into *A. dombeyanum*, although the three-ribbed abaxial petiole surfaces are rare in that species.

The leaf of *Anthurium dombeyanum* demonstrates great morphological plasticity in size and shape. A common feature of many collections is an obtuse to rounded leaf base with an aggregation of many veins in the lower few centimeters of the base. Yet plants in the same population, or even on the same individual, may commonly exhibit acute leaf bases lacking such an aggregation of veins. Comparison of *Croat 58323* and *Croat 58324* demonstrates the range of leaf bases found within a population. Inspection of the various sheets of *Croat 57707* or *Croat 58323* demonstrates this tendency within one individual. The species is also tremendously variable in size, ranging from rather tiny plants collected in exposed areas (e.g., *Vargas 3988*) to huge plants growing in more mesic habitats (e.g., *Croat 58323*).

Several collections are worthy of special mention. Two individual collections, *Croat 58366* and *Ellenberg 3538*, are from unusually low elevations, i.e., 630 m and 370 m, respectively. The Croat collection, from Cajamarca, Peru, is perhaps a distinct species, having blades that dry yellowish green rather than the more typical brown color, and a weakly glaucescent aspect to its mature leaves. The Ellenberg specimen, from Amazonas, Peru, on the road between Bagua and Nazareth, is not unusual in any manner other than its aberrant low elevational occurrence. *Sparre 19272* was also

collected at a rather low elevation (700–800 m) and is the only collection known from Morona-Santiago Province in Ecuador; its leaf blade is also unusually broad. *Vargas 6209*, from Cadena in Cuzco, Peru, is aberrant in having the peduncle only ⅔ the length of the petiole (vs. (2)7–10× longer in typical *A. dombeyanum*), although the spadix is rather immature. Two collections from near Quillabamba in Cuzco, Peru (*Croat 50962*, *50919*) differ in having the petioles 3-ribbed abaxially, whereas most, if not all, other material has petioles rounded abaxially. *Barbour 2583*, from Amazonas in Peru, is remarkable in having a spathe 4 cm broad near the base and a petiole recorded as terete. The spathe of *Croat 58192*, from San Martín, approaches the dimensions of the Barbour collection.

ECUADOR: LOJA: Cerro Campana, Vilcabamba–Yangana, Km 7, 1,900 m, 79°16′W, 4°17′S, *Lojtnant & Molau 15002* (AAU, GB); Loja–San Lucas, 2,100 m, *Asplund 18056* (S); Km 25–32, 2,200 m, *Dodson & Thien 597* (MO), *659* (MO, US, WIS); 19 km N of Loja, 2,070 m, 4°10′S, 79°10′W, *Croat 50847* (AAU, B, CM, GB, K, M, MBM, MO, QCA, SEL, US); Mollococha, 10 km W of Vilcabamba, 1,600 m, *Harling & Andersson 21769* (GB). MORONA–SANTIAGO: Gualaquiza, Misión Bomboiza, Misión Salesiana, 700–800 m, *Sparre 19272* (S). TUNGURAHUA: *Sodiro s.n.* (B); Agoyan, *Sodiro s.n.* (B; photo, MO). PERU: Without locality, *Dombey s.n.* (P). AMAZONAS: Prov. Bagua, 15.6 km E of main plaza in Bagua, 5 km above La Peca, 1,050–1,160 m, 5°33′S, 78°21′W, *Croat 58358* (MO, USM); 12 km E of La Peca (by trail), 1,700 m, *Barbour 2583* (MO); Bagua Grande, Longa Grande, Buenos Aires (Calpon), 1,420 m, *Diaz & Campos 3427* (MO); Bagua–Nazareth, 370 m, *Ellenberg 3538* (MO); Prov. Bongara, Bongara, 8 km above Pedro Ruiz Gallo (Jazan), road to Pomacochas, 1,500–1,600 m, 5°55′S, 77°53′W, *Knapp & Alcorn 7538* (MO); Río Utcubamba, SE of Naranjitos, *Gentry et al. 61375* (MO); Suyobamba, 3 km NE of Pedro Ruiz Gallo, 1,400 m, 5°55′S, 77°58′W, *Gentry et al. 61290* (MO); Chiclayo–Río Utcubamba, trail above hwy., NW of Pedro Ruiz Gallo, 1,300–1,400 m, *Young & Eisenberg 289* (MO); Moyobamba–Bagua, NW of Pedro Ruiz Gallo, 1,820 m, 5°52′S, 77°56′W, *Croat 58314* (MO); at jct. of road to Chachapoyas, NW of Pedro Ruiz Gallo, 1,440 m, 5°56′S, 77°56′W, *Croat 58321, 58324* (MO, USM, VBD), *58322* (CAS, CM, MO, NY, RSA, USM), *58323* (K, MO, RSA, SEL, US, USM); Lago Pomacocha, Moyobamba–Chachapoyas, Km 339–340, Pomacocha, 2,200–2,250 m, 5°47′S, 77°53–54′W, *Croat 58254* (MO, NY, USM), *58281* (MO); Prov. Chachapoyas, Hacienda Shani, Chachapoyas, *Cevasco s.n.* (USM). AYACUCHO: Valle de San Miguel, Media Naranja, 2,000 m, 13°13′S, 73°95′W, *Guerrera 2034* (F). CAJAMARCA: Prov. Cajamarca, Huambos, 2,200 m, *Ferreyra 8409* (NY, USM); Prov. Jaén, Río Chamaya, Bagua–Olmos, 35 km E of Pucara, 70 km W of Río Marañon bridge, 630 m, 6°0′S, 78°52′W, *Croat 58366* (AAU, C, CAS, CM, GH, K, KYO, MO, NY, SEL, U, US, USM). CUZCO: Prov. Calca, Vilcabamba, 2,700 m, *Vargas 3988* (CUZ); Prov. Convención, Choquellowanca, 1,450 m, *Vargas 12947* (CUZ); Cuzco–Kiteni, Cocalpampa, 150 km NW from Cuzco, 1,210–1,435 m, *Nuñez et al. 6816* (MO); Rosario Mayo, 950–1,200 m, *Chávez 3334, 3336* (MO), *Vargas 20674* (US); Quillabamba–Cuzco, just S of Quillabamba, 1,050–1,200 m, 12°20′S, 72°44–45′W, *Croat 50919* (CM, MO), *50962* (COL, M, MO, MY, USM); Santa Teresa–Chaullay, at Quellomayo, 139 km from Cuzco, 1,200–2,600 m, 13°08′S, 72°36′W, *Nuñez & Motocanchi 8752* (MO); Urusayhua, 1,400 m, *Chávez 507* (MO); Río Mopillo, Yupanqui–Río Apurimac, Pomobamba, 2,000 m, *Davis et al. 1261* (F, SEL); Río Urubamba, Quillabamba, 1,100 m, *Solomon 3111* (MO, F); Prov. Quispicanchis, Cadena, 1,060 m, *Vargas 6209* (CUZ); Masca Pata, Hda. Itio, 2,000 m, *Vargas 3053* (CUZ); Prov. Urubamba, Km 88–92, 2,500 m, *Vargas 3396* (CUZ); km 110 Machupicchu–Cuzco, 2,000 m, 13°09′10″S, 72°31′W, *Nuñez 8679* (MO); 2,900 m, *Nuñez 8423* (MO); Machupicchu, *Jackson & Jackson P-1* (F); 2,000 m, *Bogner 904* (K); 2,300 m, *Vargas 21642* (CUZ, MO); 2,300 m, *Zahner s.n.* (M); railway, Km 96, 2,300 m, *Palmer 181* (K); Laderas, 2,100 m, *Vargas 2982* (CUZ); Papacahua, 4 stops on railroad above Machupicchu, 2,500 m, 13°11′S, 72°30′W, *Croat 50969* (MO); Tankarpata, 2,650 m, *Vargas 13576* (CUZ, US). HUÁNUCO: Tingo María Region, Huamincha, 1,800 m, *Woytkowski 34220* (F, G, MO, UC); Prov. Huánuco, Acomayo, 2,300 m, *Woytkowski 34331* (F, MO, UC); Río Tulca, Huánuco–Tingo María, km 443, 6 km N of Acomayo, 2,450 m, 9°04′S, 76°04′W, *Croat 57842* (CAS, CM, MO, NY, RSA, SEL, US, USM). JUNÍN: Prov. Acobamba, Acobamba–Oxapampa, Carretera 20B, 23 km NE of Acobamba, 2,170 m, *Jones 9138* (LAM, MO); Prov. Tarma, Tarma–Oxapampa, 38 km NE of Tarma, on Carretera 20B, 2,226 m, *Jones 9105* (LAM); Tarma–San Ramón, 1,000–3,000 m, 11°10′S, 75°20–45′W, *Sullivan et al. 1067* (F, MO, SEL); 2,400 m, 11°10′S, 75°33′W, *Smith & Canne 5931* (B, MO); Carpapata, 2,400–2,500 m, *Cerrate 2810* (USM); Huasahuasi, 2,760 m, *Hutchison 4164* (UC, US); Huacapistana, rd. to Palca, *Weberbauer 1975, 2007, 2158* (B); Huacapistana, 1,800–2,400 m, *Killip & Smith 24328* (NY, US); Matichacra, near Huacapistana, 2,100–2,200 m, *Ferreyra 11180* (NY); 28–34 km NE of Tarma, 2,400–2,500 m, *Dillon & Turner 1354* (F, MO), *Croat 57707* (AAU, B, BM, K, MO, RSA, U, USM), *Gentry & Tredwell 37285* (MO). LA LIBERTAD: Río Santo Domingo, Piedra Grande, 1,670 m, *Macbride 3668* (F). PASCO: Prov. Oxapampa, Palmazu, 2,100 m, 10°32′S, 75°23′W, *Smith et al. 8495* (MO). SAN MARTÍN: Rioja–Pomacocha, km 291, near Amazonas border, Venceremos, 1,850 m, 5°45′S, 77°40′W, *Gentry et al. 45343* (MO); Moyobamba–Chachapoyas, Km 400–404, 1,150–1,280 m, 5°45′S, 77°29′W, *Croat 58204* (MO, USM), *58192, 58207* (MO).

Anthurium ernestii Engl., Pflanzenr., IV. 23B(Heft 21): 80. 1895.

a. Anthurium ernestii var. **ernestii**. TYPE: Peru. San Martín: Pongo de Cainarachi, *Ule 6325* (lectotype, B). Figures 124, 128–130.

Epiphytic; stem 6–20 cm long, 1–3 cm diam.; roots dense, green, whitish when dried, velutinous, 2–5 mm diam.; cataphylls subcoriaceous, 2-ribbed,

3–12 cm long, acuminate at apex, drying reddish brown to light brown (B & K yellow-red 4/10), persisting intact, eventually as reticulum of fine, straw-colored fibers with the apex remaining intact. *Leaves* erect-spreading; petioles 4–30 cm long, 3–13 mm diam., D-shaped, sulcate and with a medial rib adaxially, the margins acute, rounded to 1–5-ribbed abaxially; geniculum thicker and paler than petiole, 0.5–2.3 cm long; sheath 1.5–6 cm long; blades subcoriaceous, elliptic to oblanceolate to oblong-oblanceolate, acute to acuminate at apex (the acumen flat), attenuate to obtuse, rarely rounded at base, (25)40–60(131) cm long, (6)7–20(36) cm wide, broadest at or above the middle, the margins broadly undulate, frequently concave in the lower part of the blade; both surfaces matte to semiglossy, generally drying green; midrib broadly and acutely raised at base, becoming flat toward the apex above, acutely raised below with a prominent central ridge at base, becoming slightly convex at apex; primary lateral veins 6–15 per side, departing midrib at 30–70° angle, straight to arcuate-ascending to the margin, prominently raised near the midrib, flat to sunken near the margin above, prominently raised below, drying orangish; tertiary veins prominulous, raised on both surfaces; collective vein arising in the upper ⅓ of the blade, 5–13 mm from margin. *Inflorescences* erect; peduncle 3–25(45) cm long, 2–6 mm diam., 0.5–3(5.7)× as long as petiole, pale green, terete; spathe erect to reflexed or recurled, subcoriaceous, green to green tinged with red at base (B & K yellow-green 6/7.5), lanceolate to broadly lanceolate, 4–12 cm long, 1–3(4) cm wide, broadest near base or sometimes at or near middle, inserted at 45–80° angle on peduncle, abruptly acuminate to acute at apex, acute at base; spadix pinkish to magenta to purplish or green at anthesis, sessile, rarely stipitate to 0.5–1 cm, cylindroid, slightly tapered, erect, slightly curved, 3–11(20) cm long, 3–14 mm diam.; flowers 4-lobed, 1–1.9 mm long, 1.4–1.7 mm wide, the sides sigmoid; 5–8(17) flowers visible in principal spiral, 7–11(16) in alternate spiral; tepals matte, densely papillate; lateral tepals 0.4–1 mm wide, the inner margins straight to convex, the outer margins 2–3-sided; pistils raised, the exposed portion rectangular to squarish, often reddish violet, darker than tepals; stigmas slitlike to ellipsoid, 0.2–0.6 mm long; stamens emerging in a regular sequence, the laterals preceding the alternates by up to 27 spirals, the 3rd stamen preceding the 4th by up to 25 spirals; filaments ca. 0.6 mm long, 0.8 mm wide; anthers purplish or pinkish to pinkish white, 0.2–0.7 mm long, 0.4–0.6 mm wide, inclined over and obscuring the pistil; thecae ellipsoid, not divaricate; pollen pale yellow fading to white. *Infructescence* spreading; spathe withered; berries red-violet to violet (B & K purple 3/10–4/10), subglobose to obovoid, rounded at apex, 4–10 mm long, 3–6 mm diam.; seeds 1–2 per berry, obovoid, 2–4 mm long, 1.5–2.5 mm diam., creamy brown, with sticky appendage at apex; mesocarp grayish, juicy, somewhat mealy.

Anthurium ernestii var. *ernestii* ranges throughout western Amazonia, from southern Colombia (Putumayo) to Peru (Amazonas, Loreto, San Martín, Huánuco, Pasco, and Madre de Dios), and western Brazil (Acre and Amazonas as far east as the Rio Madeira), mostly below 500 m (rarely to 800 m) in tropical moist, premontane wet, and tropical wet forest life zones.

This species is recognized by its fine, thin, pale brown to pale tan network of cataphyll fibers with the uppermost cataphylls often skeletally intact or nearly so and by its oblanceolate leaf blades which generally dry green or greenish brown with the primary lateral veins more or less orange (especially on the lower surface). Also characteristic is the generally short peduncle and especially the cylindroid spadix which is about 5–8× (rarely to 13×) longer than broad and often has a minutely prickly appearance owing to the tight clusters of stamens and the upturned tepals on dried collections (or more rarely the exserted styles).

Like most of the widespread species of sect. *Pachyneurium*, *A. ernestii* var. *ernestii* is quite variable overall and is not easily understood when only specimens representing a portion of the geographical and/or morphological extremes are at hand. Among the most variable characters for the species are spadix and fruit color. Spadix color has been reported as greenish yellow, pale green, pale olive-green, orange-buff, pink, pinkish, yellowish pink, grayish pink, light purplish pink, reddish, reddish brown, light pink-brown, purplish white, light violet, violet, pale purple, purple, reddish cream, or cream turning magenta. It is generally not a dark color (at least at anthesis), nor a color easily qualified. As in many species of *Anthurium*, the spadix often changes color during the course of anthesis. Fruits are variously described as violet, dark violet, bright purple, purple, or red.

The morphological plasticity of *Anthurium ernestii* is rather remarkable and is geographically clinal in nature, with plants increasing in size from north to south. In Ecuador, most notably in Napo, plants tend to be relatively small with short petioles and small inflorescences, and leaves mostly drying distinctly green with the characteristic or-

angish primary lateral veins. Additionally, leaf blades are proportionately narrower in Ecuador (averaging 4.6× longer than broad) than in Peru (averaging 3.4× longer than broad).

Peru is believed to be the center of distribution for the broadly interpreted taxon comprising *Anthurium ernestii*, and the departments of Loreto (including newly created Ucuyali Department), San Martín and Madre de Dios in particular harbor the greatest amount of morphological diversity. This is particularly true of the Río Huallaga and Río Ucayali basins (especially the region between the east banks of the latter and Acre, in Brazil).

In Loreto, and to a lesser extent in Huánuco and Pasco, the specimens seen exhibit an overall tendency toward a significant increase in size and show a greater departure from the "typical" condition of leaves drying green or greenish. Many dry brown or brownish green, but still largely exhibit the orangish primary lateral veins.

Anthurium ernestii typically has a peduncle about twice as long as the spadix, but in San Martín Department a few collections from Distrito Tocache Nuevo are very large in overall size and have peduncles 30–42 cm long and about 3× longer than the spadix. The number of flowers per spiral for the spadices of these plants represents the higher range limit for the taxon.

Peduncle length in relation to petiole length is greater in the northern part of the range (a collection from southern Colombia has a peduncle 5.7× longer than the petiole, the greatest disparity observed). In Peru, the peduncles are normally about equally as long as the petioles. Overall, the peduncle is commonly no more than 3× longer than the spadix.

Anthurium ernestii appears to be most closely related to *Anthurium galactospadix*. It differs at once from *A. ernestii* in having the spathe longer than the stouter spadix, and in having more (13–28) flowers per spiral.

Anthurium ernestii is apparently also closely allied to *A. uleanum*, which is largely sympatric. In general, *A. uleanum* may be distinguished from *A. ernestii* by its more slender, glaucous-looking spadix, longer peduncle and petioles, and leaf blades which mostly dry brown. In addition, *A. uleanum* lacks the characteristic pale, skeletally intact cataphylls and orangish drying primary lateral veins of *A. ernestii*. Occasionally, spadices of dried collections of what are believed to be *A. ernestii* var. *ernestii* may have a thin, waxy layer when they are very young, but this is usually soon sloughed off, at least before anthesis. *Harling 1118* is an example.

Anthurium ernestii comprises two varieties, with var. *ernestii* encompassing the range of the species. Variety *oellgaardii*, which occurs in central Ecuador in Pastaza, differs from the typical variety in having a proportionately more slender, tapered spadix, a spreading, rather than erect, peduncle, and leaves which dry bright green. In Ecuador, peduncle length for var. *ernestii* ranges up to the lower limit for var. *oellgaardii*, but rarely exceeds it and is often much shorter.

A source of possible confusion is a Field Museum photograph of the type of *A. ernestii*. It depicts two different herbarium specimens. The one on the left (*Ule 6325*) is the lectotype of *A. ernestii*. The specimen on the right (apparently now lost) is labeled *Ule 5776* and closely resembles the specimens discussed under *A. galactospadix* (*Cid & Nelson 2563*, *Prance et al. 7471*). The latter specimen consists of part of a leaf blade, a petiole, and an inflorescence. This specimen apparently represents a mixed collection since a note on the specimen indicates that *Ule 5776* is actually a Gesneriaceae and that the specimen in the photograph is possibly *Ule 5788*. However, *Ule 5788*, represented by a plant at Geneva, is a species with a much shorter petiole than the one depicted in the photograph.

BRAZIL. ACRE: Mpo. Cruzeiro do Sul, Mpo. Caramari Amazonas, Rio Jurua, N of Cruzeiro do Sul, 150 m, 7°137′S, 72°136′W, *Croat 62482* (F, MO, TEX), *Croat 62492* (MO); Rio Moa, Boiador, 150 m, 7°37′S, 72°37′W, *Croat & Rosas 62302*, *62303* (CAS, INPA, MO), *62408* (INPA, MO). AMAZONAS: Boca do Acre, *Prance et al. 2338* (INPA); Rio Jurúa, *Ule 5788* (G); Mpo. Humayta, Rio Madeira, Tres Casas, *Krukoff 6097* (NY), *Krukoff 6496*, *6548* (GH, NY), *Krukoff 6547* (GH, K, NY). COLOMBIA: PUTUMAYO: El Wiskey, 13 km S of Umbria, vic. Finca Santa María, 300 m, *Plowman 2066-A* (F). ECUADOR: MORONA–SANTIAGO: Patuca, 600 m, *Harling 1118* (S); Río Paute, Méndez, 700 m, *Harling 1090* (S); Mendez–Paute, 600 m, 2°44′S, 78°19′W, *Lojtnant & Molau 14549* (AAU); Yurupaza, 600 m, 2°40′S, 78°14′W, *Harling 984* (S). NAPO: 3 km E of Anangu, Communa San Isla, 260 m, 0°29′S, 76°21′W, *Lawesson et al. 39799* (AAU); Puerto Bolívar–Comunidad Siona, S of propriety of Victoriano Criollo, *Jaramillo & Coello 2850* (AAU, QCA); Puerto Napo–Puerto Misahuallí at jct. with Río Napo, 3.5 km E of Puerto Napo, 1°02′S, 77°47′W, *Croat 58885* (MO); 2–5 km SSW to WSW of San Pablo de las Secoyas, path to Shushufindi, 300 m, 0°15′S, 76°21′W, *Brandbyge et al. 32548*, *32796*, *33359*, *33412*, *36222* (AAU); trail to Shushufindi, E of San Pablo de Las Secoyas, *Jaramillo & Coello 2685* (AAU, QCA); N of San Pablo de Las Secoyas, *Jaramillo & Coello 2804* (AAU, QCA); Orellana, Sector Huashito, 20 km N of Coca, 250 m, 0°20′S, 77°05′W, *Gudino 211* (MO); San Pueblo, 35 mi. E of Lago Agrio, *Hodgson 165* (K); Lago Agrio–Puerto El Carmen de Putumayo, vic. Tarapoa, 76 km E of Lago Agrio, 240 m, 0°07′N, 76°23′W, *Croat 58632* (MO); Río Aguarico, Cuyabeno,

S of the river, 200 m, 0°17′S, 75°53′W, *Holm-Nielsen et al. 21543* (AAU, MO); Dureno, *Pinkley 245* (ECON), *Jaramillo & Coello 3029* (QCA); Lago Agrio, 7.2 km S of Río Aguarico, 270 m, 0°02′N, 76°51′W, *Croat 58643A* (MO, NY, QCA), *58642* (MO, QCA); 350 m, *58689* (MO, QCA); 17.3 km N of Lago Agrio, 0°07′N, 76°50′W, *Croat 50304* (MO); Lagunas de Cuyabeno, 300 m, 0°01′S, 76°11′W, *Brandbyge et al. 33983* (AAU), *36079* (AAU, MO); 265 m, *Poulson 80804* (AAU), *Nielsen 76092* (AAU); Reserva Faunistica de Cuyabeno, N of Laguna Grande, 265 m, 76°11′W, 0°01′N, *Balslev et al. 84417* (AAU); Río Shushufindi, near confluence with Río Aguarico, 300 m, 0°18′S, 78°20′W, *Balslev 4831* (NY); Tena–Puyo, 5 km S of bridge over Río Napo, 510 m, 1°05′S, 77°47′W, *Croat 58921* (MO); Tena, *Asplund 9423* (S); 5.7 km W of Tena, 500 m, 00°01′S, 77°51′W, *Croat 58855* (MO, QCA); Río Cotapino, 50 km NE of Tena, Cotapino, 500 m, *Harling et al. 7023* (GB); Río Arajuno, Hacienda Aguinda, 450 m, 1°07′S, 77°36′W, *Marles EE 13A* (F); Río Due, Baeza–Lago Agrio, Km 65, trail to Chuscuyacu, "Zona Reserva Ecológica Cayambe–Coca," *Jaramillo & Coello 3061* (AAU); Río Napo, Ahuano, 1°04′S, 77°31′W, *Lugo 245* (GB, MO); Parque Nacional Yasuní, Anangu, 260–350 m, 0°31–32′S, 76°23′W, *Lawesson et al. 39473* (AAU), *Luteyn & Mori 8530* (NY), *Luteyn et al. 8700* (MO); Pozo petrolero Daimi 2, 200 m, 0°55′S, 76°11′W, *Cerón & Hurtado 4088, 4238* (MO); near confluence with Río Aguarico, Ballesteros (military post), *Harling et al. 7368* (GB, MO); confluence of Río Coca and Río Napo, Coca, 350 m, *Harling & Andersson 11798* (GB); Coco–Las Sachas, 0°25′S, 76°55′W, 250 m, *Ceron et al. 2425* (MO, QCNE); Coca, Río Payamino, 350 m, *Harling & Andersson 11928* (GB); Payamino, Reserva Floristica "El Chuncho," 0°30′S, 77°1′W, 250 m, *Ceron et al. 2275* (MO, QCNE), *2286* (MO, QCNE), *2516* (MO, QCNE); E of Puerto Misahuallí, 400 m, *Besse et al. 1194* (SEL); 8 km below Puerto Misahuallí, 1.5 km S of Río Napo, 450 m, 1°04′S, 77°36′W, *Palacios et al. 448* (MO, NY, QAME, QCNE); Santa Rosa, 32 km E of Tena, 0°01′N, 77°30′W, *Lugo 2065* (GB); Río Napo–Tena, 8 km SE of Tena, Shinguipino, 480 m, *Grubb et al. 1530* (K, NY); Jatún Sacha Biological Reserve, 8 km ESE of Puerto Misahuallí, 400 m, 1°04′S, 77°37′W, *Miller et al. 2198, 2200* (MO); 400 m, *Cerón 1330* (MO, QCNE), *1742* (MO, QCNE), *1694* (MO, QCNE), *2578* (MO, QCNE), *2671* (MO, QCNE); Río Pacuno, Bimbino, 300 m, 0°40′S, 77°20′W, *Whitmore 746* (K); Río Putumayo at Colombian frontier, Baeza–Puerto El Carmen de Putumayo, 43.7 km SE of Lago Agrio, 16.9 km SE of Dureno, 2.1 km W of Guarumo, 240 m, 0°7′N, 76°39′W, *Croat 58591* (MO, QCA); Río Wai si aya, northern tributary of Río Aguarico, 300 m, 0°15′S, 76°21′W, *Brandbyge et al. 32652, 32653, 36195, 36199* (AAU); Yasuní Nacional Parque, 200 m, 0°55′S, 76°11′W, *Cerón & Hurtado 3866* (MO), 230 m, 0°52′S, 76°05′W, *Cerón 3345* (MO); Río Yasuní, 180–200 m, 1°05′S, 75°35′W, *Lawesson et al. 43314, 43320* (AAU); Lago Garza Cocha, 200 m, *Lawesson et al. 43500* (AAU); 80 km upriver from Nuevo Rocafuerte, 225 m, *Foster 3671, 3703B* (F), *Alarcon 47* (QCA); Cantón Lago Agrio, Dureno, 350 m, 0°2′S, 76°42′W, *Cerón 347* (MO), *Cerón & Cerón 3131* (MO); Cantón Orellana, sector Huashito, 20 km N of Coca, 250 m, 0°20′S, 77°05′W, *Rubio 259* (MO); Cantón Tena; Río Blanco community at headwaters of Río Huambuno, 6 km NNW of Ahuano, 440 m, 1°00′S, 77°40′W, *Kohn 1136* (MO). PASTAZA: Puyo–Diez de Agosto, 8.2 km NE of Diez de Agosto, 970 m, 1°27′S, 77°51′W, *Croat 59051* (MO, QCA); Río Bobonaza, oil exploration camp Chicirota, 300 m, 2°22′S, 76°40′W, *Oellgaard et al. 35301* (AAU); Río Capihuari, tributary of Río Pastaza, 285 m, 2°30–31′S, 76°50–55′W, *Oellgaard et al. 35102* (AAU); Río Curaray, S side of river, mouth of Río Queramo, 230 m, 1°30′S, 76°32′W, *Neill & Palacios 6775* (MO, NY, QAME), *Palacios & Neill 719* (K, MO, QAME); N side of river, las lagunas Potoamo, 230 m, 1°30′S, 76°30′W, *Neill & Palacios 6818* (MO, NY, QAME); Lorocachi, 200 m, 1°36–38′S, 75°58–59′W, *Jaramillo et al. 30918, 31150, 31568, 31584* (AAU), *30965B* (MO), *31188* (AAU, MO); Centro–Oriente, Tzapino, *Jaramillo & Coello 3602* (QCA), *3644* (QCA); Tiwaeno, *Jaramillo & Coello 3207* (QCA). PERU. AMAZONAS: Prov. Bagua, Río Cenepa, Isla de Chigkan, 330 m, *Kayap 320* (MO); Quebrada de Apigkagentsa, 720 m, *Kayap 602* (MO); Quebrada Etseketai, 240 m, *Kayap 841* (MO); Huampami, ca. 5 km E of Chávez Valdivia, 200–250 m, 4°30′S, 78°30′W, *Ancuash 1095, 1260, 1336* (MO), *Berlin 2046* (MO), *2080* (MO, PMA), *Kujikat 72, 161, 237, 302* (MO); S of Huampami, S of river, 266–283 m, *Berlin 1689* (MO); S of Huampami, trail to Sasa, 250 m, *Berlin 1707* (MO); above Quebrada Tuhusik, 5 min. down river from Chávez Valdivia, 230–270 m, *Berlin 560* (MO); Río Cenepa–Quebrada Kayamas, 270–300 m, *Berlin 514* (MO); Río Huampami, 250–280 m, *Kayap 1251, 1339* (MO); Río Marañon, above Pongo de Manseriche, 200 m, *Wurdack 2456* (US), *Mexia 6132a* (UC); Río Santiago, E of the river, Galilea, 180 m, *Huashikat 71* (MO); Quebrada Caterpiza, 2–3 km behind community of Caterpiza, 65 km N of Pinglo, 200 m, 3°50′S, 77°40′W, *Huashikat 1793, 2025, 2086, 2275* (MO), *Tunqui 395, 690, 712, 840* (MO); 1–2 km below La Poza, 180 m, *Leveau 3, 264, 306, Peña 84* (MO); 400 m behind La Poza, 180 m, *Huashikat 142* (MO); behind house of Jaime Braga, *Leveau 59* (MO); Chiriaco–Puente Venezuela, 43 km NE of Chiriaco, 350–800 m, *Barbour 4429* (MO); E of Huampami, trail to Shaíme, 200–600 m, *Berlin 1918* (MO); trail E from La Peca into Serranía de Bagua, 1,000–1,400 m, *Gentry et al. 23090* (MO); Quebrada Wampushik, 310 m, *Kayap 936* (MO); Mesones–Muro Hwy., 8 km E of Montenegro, at km 286, 8 km E of Montenegro, 650 m, 5°20′S, 78°20′W, *Hutchison & Wright 3764* (UC). HUÁNUCO: Tingo María Region, Bella Durmiente, 700 m, *Ferreyra 13808* (USM); Tingo María–Monsón, Cuevas de Gucharo "Parque Nacional Tingo María," Río Patay, 650 m, 9°21′S, 76°12′W, *Croat 57930* (MO); Prov. Leoncio Prado, Dtto. Rupa Rupa, Río Huallaga, 700--800 m, *Croat 21023* (MO); 750–800 m, *Plowman & Ramirez 7568* (F, MO); Tingo María Region, 675 m, *Croat 50978* (MO, RSA), *Solomon 3388* (MO); W of Tingo María, 700–800 m, *Schunke 10516* (MO); Prov. Pachitea, W of Codo de Pozuzo, 500–1,000 m, 9°40′S, 75°28′W, *Foster 9217* (MO); Bosque Nacional de Iparia, Río Pachitea, 1 km above Tournavista, near Miel de Abeja, 300–400 m, *Schunke 1827* (F, NY, US), *2240* (F). LORETO: Río Ampiyacu, Pucaurquillo, *Davis et al. 819* (F, SEL); Prov. Alto Amazonas, Balsapuerto, 150–350 m, *Killip & Smith 28695* (F, NY, US); Río Huallaga, Lagunas, *Croat 17838* (MO, USM); Yurimaguas, 135–200 m, *Ferreyra 4949* (USM), *Killip & Smith 28074* (NY, US); Puerto Arturo, below Yurimaguas, 135 m, *Killip & Smith 27733* (NY, US); Río Paranapara, Yurimaguas, less than 500 m, *Croat 17931* (MO); Río Pastaza, Andoas, 180 m, 2°55′S, 76°25′W, *Croat 51255* (CM, MO), *Vásquez 4435* (MO),

Vásquez & Jaramillo 848 (MO, RSA), *Vásquez et al. 2985* (MO); Prov. Loreto, San Jose de Parinari, 150 m, 4°32′S, 74°30′W, *Vásquez & Jaramillo 3326* (MO); Pucayacu (native community Shimaco–Urarina), *Vásquez 6036* (MO); Río Marañon, 1 hr. above Saramuro, 4°40′S, 75°00′W, *Diaz & Ruiz 872* (MO, SEL); Río Samaria, Atuncocha, *Vásquez et al. 4362* (MO); Río Santiago, 200 m, *Mexia 6142a* (MC, UC); Campamento 2–Flor de Yarina, 140–160 m, 5°02′S, 74°30′W, *Gentry et al. 38068* (MO); Prov. Maynas, Sacarita de Yanayacu, 90 m, *McDaniel & Rimachi 25633* (MO), *25668, 25684* (IBE, MO); Santa María de Nanay, Quebrada Yarina, 150 m, 3°55′S, 73°40′W, *Vásquez et al. 12200* (MO, US); Iquitos Region, Río Maniti, Recreo, NE of Iquitos, 115 m, 3°42′S, 72°50′W, *Vásquez & Jaramillo 1139* (MO); Río Itaya, Sanangal, 120 m, 4°10′S, 73°20′W, *Vásquez et al. 315* (MO); Quebrada Tahuayo, above Tamishiyaco, *Croat 19708, 19744* (MO); Río Amazonas, village Yanamono, near mouth of Río Napo, 150 m, 3°25′S, 72°50′W, *Croat 50125* (from a live plant collected by A. Gentry) (MO); Yanamono, Explorama Tourist Camp, *Croat 61762* (AMAZ, MO, WIS), *Gentry et al. 31496, 36637, 61833* (MO), *Gentry 29912A* (MO); Mariscal Castilla, 106 m, 3°55′S, 70°30′W, *Vásquez & Jaramillo 9344* (MO); Río Gueppi, tributary of Río Putumayo, 8 km from mouth of river, Puerto Peru–Río Napo trail, 200 m, *Gentry et al. 21963* (F); Explorama Inn, ca. 2 km W of Indiana, 130 m, *Gentry et al. 55988* (MO); Río Napo, *Croat 20188* (MO); Río Yaguasyacu, trib. of Río Ampiyacu, Brillo Nuevo, 2°40′S, 72°00′W, *Balick et al. 1040* (GH); Prov. Maynas, Dist. Iquitos, Iquitos Region, Río Momón, Quebrada Momoncillo, 200 m, 3°43′S, 73°20′W, *Croat 51223* (BM, CAS, MO, USM); Prov. Maynas, Dtto. Amazonas, Quebrada Yanamono, below Indiana, 120–140 m, *Rimachi 1198* (MO). MADRE DE DIOS: serranía across Río Alto Madre de Dios from Shintuya, Pantiacolla, 480–840 m, *Gentry et al. 27359* (MO); confluence of Río Tambopata and Río La Torre, 39 km SW of Puerto Maldonado, 12°50′S, 69°20′W, *Smith et al. 118, 610* (US), *638* (NY, US), *Smith 230* (US), *Smith 307* (MO, US); Manú National Park, Cocha Cashu Uplands, 400 m, 11°45′S, 71°0′W, *Nunez 5549* (CUZ, MO, USM); Río Manu, 350–400 m, *Davidson 117* (MO), *Foster 5811* (F), *Foster & Terborgh 6482* (F); Tambopata Wildlife Reserve, 30 km S of Puerto Maldonado, 260 m, 12°15′S, 69°17′W, *Young & Stratton 120, 141* (MO), *Young 18* (MO, NY); Prov. Manu, Río Palotoa (Río Panticolla), tributary of Alto Madre de Dios, NW of Shintuya, 500 m, *Foster & Terborgh 6749* (F). PASCO: Prov. Oxapampa, Iscozazin–Villa America, 350–450 m, 10°11′S, 75°15′W, *Smith 2854* (MO, US); Palcazú Valley, Iscozacin, less than 500 m, *Salick 7265* (MO); Río Pichis, 10 km downriver, E of island, Puerto Bermudez, Reserva Musmuqui "Nuevo Hoboken," *Foster & Wright 8041, 8127* (F), *Kuntze 2006* (NY). SAN MARTÍN: Tocache Nuevo–Juanjui, 84 km S of Juanjui, 14.1 km beyond bridge over Río Pulcache, 600 m, 7°41′S, 76°40′W, *Croat 58029, 58031A* (MO), *58030* (CM, MO, USM); Pongo de Cainarachi (Shanusi), *Ule 6325* (B); Prov. Mariscal Cáceres, Madre Mía, 760–880 m, *Boeke & Ramírez 1281* (NY); Prov. Mariscal Cáceres, Dtto. Tocache Nuevo, Tocache Nuevo, E of bridge, 500 m, *Schunke 7790* (MO); Quebrada de Cañuto, 500 m, *12107* (IBE); Colegio Agropecuario de Tocache, 400 m, 8°13′S, 76°32′W, *Croat 57994* (CAS, F, DUKE, GH, M, MO, RSA, SEL, TEX, US, USM), *57995* (B, K, MO, USM); 5 km S of Cachaco, 42 km N of Tocache Nuevo, 330 m, 7°58′S, 76°38′W, *Croat 58048* (MO, NY, USM); Fundo de Las Flores, 550–600 m, 8°10′S, 76°33′W, *Croat 50991* (CM, MO), *50992* (F, MO, SEL), *50993* (MO, NY), *50994* (B, CM, IBE, K, M, MO, RSA, USM); Fundo Geoglifico del Sr. Luis Luden, Quebrada de Ishichimi, 400 m, *Schunke 8107* (MO); Granja Santa Ysabel, old rd. to Limón, 400 m, *Schunke 10326* (MO); Palo Blanco, W of bridge, 600–700 m, *Schunke 5624* (F, NY, U, US); Palo Blanco, E of bridge, road to Shunte, 500–800 m, *Schunke 7391* (CM, MO); Quebrada Pucayacu, chacra del Sr. Alfredo Sinarahua, 400 m, *Schunke 12001* (IBE); Río Huallaga, W of Escuela de Balsa Probana, 400 m, *Schunke 3637* (COL, F, NY, US); 1–2 km downriver from Tocache Nuevo, Miramar, 500 m, 8°10′S, 76°28′W, *Plowman et al. 11417* (F, USM); Quebrada de Tanta, *Schunke 4045* (F); Río Tocache, Fundo Melodia, road to Shunte, 800 m, *Schunke 7496* (CAS, MO); Río de La Plata, 550–650 m, 8°10′S, 76°25′W, *Croat 51000, 51029, 51033, 51035, 51041* (MO), *51002* (MO, USM); 5 km NE of bridge over Río Huallaga, Fundo del Sr. Manuel Gatica, less than 100 m, 8°08′S, 76°23′W, *Croat 57986* (MBM, MO, USM), *57987* (CM, MO, RSA, USM), *57988* (F, MO, P, US, USM); Fundo del Sr. Manuel Gatica, 660–700 m, *Schunke 12136, 12138, 12186* (MO); NE of Tocache Nuevo, 400–600 m, *Schunke 8354, 8372, 8373, 8375* (F, MO), *8376* (F, MO, NY). UCAYALI: Prov. Ucayali, Río Pisqui, 7°45′S, 75°01′W, *Tessman 3249* (NY); Prov. Colonel Portillo, Km 99 on Carretera Federico Basadre, Arboretum Von Humboldt, 350 m, 8°45′S, 75°05′W, *Díaz et al. 680* (K, MO); Arboretum Von Humboldt–Puerto Inca, 5 km E of Pucallpa–Tingo María road, Km 86, less than 500 m, 8°17′S, 74°58′W, *Croat 51051* (MO); Bosque Nacional de Iparia, NW of Río Ucayali, 1 km below Iparia, 250 m, 9°12′S, 74°30′W, *Schunke 2783* (F, NY).

b. Anthurium ernestii var. **oellgaardii** Croat, var. nov. TYPE: Ecuador. Pastaza: between oil exploration camp Chichirota & Destacamento Cabo Pozo, 300 m, 2°25′S, 76°39′W, *Oellgaard et al. 34881* (holotype, MO 3039089; isotypes, AAU, QCA). Figure 131.

Differt a var. typicum pro pedunculo longiore et spadice graciliore elongatoque.

Description based on dried material only. Epiphytic; stem 1–1.5 cm thick; roots dense, whitish or brownish, velutinous, moderately short, 1–3 mm diam.; cataphylls subcoriaceous, lanceolate, unribbed, 5–8 cm long, acuminate at apex, tan, persisting as reticulum of fine and dilacerated fibers. *Leaves* erect-spreading; petioles 7–15 cm long, 3–6 mm diam., D-shaped, sulcate with a prominent medial rib and erect margins adaxially, 3–5-ribbed abaxially; geniculum thicker than petiole, 0.5–1 cm long; sheath 3–5.5 cm long; blades subcoriaceous, obovate to oblanceolate-elliptic, short-acuminate at apex, gradually attenuate toward the base, acute to obtuse at base, 54–87(100) cm long, 18–34 cm wide, broadest above the middle, the margins broadly undulate; midrib acutely raised

above, obtusely raised and faintly reddish below; primary lateral veins 10–16 per side, departing midrib at 30–50° angle, straight to arcuate-ascending to the margin, prominently raised above, less so below; tertiary veins raised, prominulous; collective vein arising in the upper ⅓ of the blade, raised above and below, prominulous, 2–10 mm from margin. *Inflorescences* spreading-pendent; peduncle 23–54 cm long, 3–9 mm diam., 2.2–4.5(5.9)× as long as petiole, terete; spathe reflexed, subcoriaceous, greenish, sometimes tinged with violet-purple, oblong-oblanceolate, 5–30 cm long, 0.9–3.5 cm wide, inserted at 40–70° angle on peduncle, acuminate at apex, acute at base; stipe 5–20 mm long in front, 1–10 mm long in back; spadix purple, cylindroid, slightly tapered, curved, erect, 7–8 cm long, 4 mm diam. near base, 3 mm diam. near apex; flowers 4-lobed, 1.2–1.5 mm long, 1.2–1.5 mm wide, the sides sigmoid; 5–6 flowers visible in principal spiral, 10–12 in alternate spiral; tepals minutely papilate, pale-punctate; lateral tepals 0.8 mm wide, the inner margins rounded, weakly scarious, minutely erose, the outer margins straight to rounded, 2-sided, paler; stigma oblong-ellipsoid, 0.3–0.7 mm long, 0.1–0.3 mm wide; anthers 0.5 mm long, 0.5 mm wide; thecae oblong-ellipsoid, slightly divaricate. *Infructescence* pendent; spathe persisting; spadix 7–60 cm long, 0.7–3 cm diam.; berries dark violet-purple in upper ⅓ becoming whitish toward the base, subglobose to cylindroid, 5–10 mm long, 3–4 mm diam.; pericarp with white raphide cells; seeds 2.8–4 mm long, 1.5–1.9 mm wide, 1.0–1.2 mm thick, with a gelatinous, transparent appendage at both ends.

Anthurium ernestii var. *oellgaardii* is known at present only from east central Ecuador in the province of Pastaza in the vicinity of the type locality on the Río Bobonaza and Río Bufeo at about 300 m in a tropical moist forest life zone. Some of the collections are reported from periodically flooded forest dominated by *Mauritia* palms.

This variety is distinguished by its large, broadly oblanceolate blades, which dry green with reddish brown or yellowish major veins and are attenuate at the base, and especially by its long-pedunculate inflorescence which is spreading-pendent at anthesis and produces a stout purple infructescence to 60 cm long and 3 cm diam. in fruit. It is noteworthy that only the type specimen has an infructescence of such large dimensions; all others are substantially more slender.

This variety shares most features of the typical variety, except the slender, tapered spadix. The latter differs in its proportionally shorter, cylindroid, spadix, generally shorter peduncles (in relation to petiole length) which are erect, and blades which usually dry brownish or, if greenish, very rarely clear green.

Anthurium ernestii var. *oellgaardii* can also be confused with *A. uleanum*, which has similar leaves, a long peduncle, and a similar, tapered inflorescence. That species differs in having tepals which bear a waxy, powderlike, grayish white covering on drying, and leaves which dry brownish. In contrast, the tepals of *A. ernestii* var. *oellgaardii* are minutely granulose and glossy on drying, and the leaves dry green.

Most of the specimens examined are of fruiting material, and the upper limits of flowering spadix length are not known.

This variety is named in honor of Benjamin Oellgaard, who participated in several expeditions to Ecuador and who made all known collections of var. *oellgaardii*.

ECUADOR: PASTAZA: Río Bobonaza, Cachitama–outlet of Río Bufeo, 300 m, 2°20′S, 76°40′W, *Oellgaard et al. 34733, 34735, 34737* (AAU); Destacamento Cabo Pozo–oil exploration camp Chichirota, 300 m, 2°25′S, 76°39′W, *Oellgaard et al. 34881* (AAU, MO), *34882* (AAU); Destacamento Cabo Pozo–La Boca, near outlet to Río Pastaza, 275 m, 2°30–35′S, 76°38′W, *Oellgaard et al. 34933, 34937* (AAU); Río Bufeo, N tributary of Río Bobonaza, 300 m, 2°20′S, 76°40′W, *Oellgaard et al. 34764, 34801* (AAU), *34769* (AAU, MO).

Anthurium eximium Engl., Bot. Jahrb. Syst. 25: 412. 1898. TYPE: Costa Rica. Puntarenas: in forest near Punta Mala, *Tonduz 6768* (lectotype, BR; isolectotype, CR). Figures 125, 132.

Epiphytic; stem elongate, 10–100 cm long, ca. 1 cm diam.; roots ascending to descending, pale green, pubescent, moderately elongate, somewhat tapered, 3–5 mm diam.; cataphylls subcoriaceous, narrowly lanceolate, 3.7–10 cm long, acute at apex with a subapical apiculum, yellowish green, drying brown, persisting intact, eventually deciduous. *Leaves* spreading; petioles 7–12 cm long, 6–7 mm diam., D-shaped to subterete, broadly to narrowly sulcate adaxially, the margins blunt or sharp, not raised, abaxially rounded to 3-ribbed; geniculum thicker and paler than petiole, 0.5–1 cm long; blades subcoriaceous, narrowly oblanceolate, long-acuminate at apex (the acumen apiculate), narrowly acute to acute to obtuse or narrowly rounded at base, 23–80 cm long, 3.3–11.5 cm wide, broadest above the middle, the margins weakly undulate;

upper surface weakly glossy to matte, medium green, lower surface weakly glossy to semiglossy, paler, drying matte, greenish; midrib obscurely and obtusely angular at base, becoming acutely raised toward the apex above, higher than broad at base, becoming round-raised toward the apex, conspicuously paler than surface below; primary lateral veins 10–12 per side, departing midrib at 40–45° angle, weakly arcuate to the collective vein, sunken above, raised below; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins obscure above, slightly darker than surface below; collective vein arising from near the base, sunken above, raised below, equally as prominent as primary lateral veins, 1–4 mm from margin. *Inflorescences* spreading, shorter than leaves; peduncle 29–32 cm long, 3–5× as long as petioles, green tinged reddish, terete; spathe spreading to reflexed, green, lanceolate-ovate to ovate, 5–7.7 cm long, 2–2.6 cm wide, clasping at base; spadix creamy white to yellow to grayish or brown, cylindroid to clavate, held at 90° angle to peduncle, 4.5–6 cm long, 8–10 mm diam. near base, 9 mm diam. near apex; flowers rhombic, 1.2–1.6 mm long, 1.3–1.8 mm wide; 10–12 flowers visible in principal spiral; tepals matte, densely papillate; lateral tepals 0.8–1.1 mm wide, the inner margins straight, the outer margins 2-sided; stigma ellipsoid, 0.3–0.4 mm long; stamens emerging somewhat irregularly in a complete sequence, the laterals preceding the alternates by 1–2 spirals; anthers pale white, 0.6–0.7 mm long, 0.5–0.6 mm wide; thecae oblong, not divaricate; pollen yellow, faintly aromatic at anthesis. *Infructescence* to 13 cm long, 1.5–1.7 cm diam.; berries pinkish to bright red, obovoid, ca. 4.6–7 mm long, 4–5 mm diam.; seeds 2 per berry, yellow, oblong, slightly flattened, 2.5–3.1 mm long, 1.2–1.5 mm diam., 0.9–1.2 mm thick.

Anthurium eximium is endemic to Costa Rica and is found strictly on the Pacific slope, in tropical wet forest formation from sea level to 800 m.

This species can be distinguished by the oblanceolate, epunctate leaves, persistent cataphylls, clasping, lanceolate spathe, cylindrical to clavate spadix, and bright red berries.

Anthurium eximium most closely resembles *A. bradeanum* and *A. spathiphyllum* (which are both restricted to the Atlantic slope), but differs from both by having entire cataphylls. *Anthurium bradeanum* also differs in having typically more elliptic leaf blades and 16–20 flowers per principal spiral (10–12 in *A. eximium*). *Anthurium spathiphyllum* also differs from *A. eximium* in having leaf blades with 20–30 primary lateral veins per side (vs. fewer than 13 in *A. eximium*).

In his monograph, Engler (1905) cited *Anthurium eximium* as a synonym of *A. consobrinum*. The leaf shapes in both species are very similar, but *A. eximium* has the collective vein arising from near the base, while *A. consobrinum* has the collective vein arising from about the middle. In addition, Schott's illustration of *A. consobrinum* clearly shows a long, slightly tapered spadix with pistils and berries greatly exceeding the tepals. *Anthurium consobrinum* is a common species of the Atlantic lowlands, and numerous collections are consistent with Schott's drawing. The berries of *A. consobrinum* are white with purple, pink, or orange apices as opposed to the solid bright red berries of *A. eximium*.

Anthurium eximium is a member of sect. *Pachyneurium* despite certain features it shares with sect. *Calomystrium*, including the thick, persistent, intact cataphylls, and the presence of linear raphide cells on both blade surfaces.

COSTA RICA. PUNTARENAS: 2.5 mi. SE of Golfito, along hwy. from Río Claro to Golfito, 60 m, 8°36′N, 83°4′W, *Croat 67622* (MO); Punta Mala, *Tonduz 6768* (BR, CR); Palmar Norte, 100–200 m, *Croat 35121* (MO); Santo Domingo de Golfo Dulce, *Tonduz 7260* (BR, CR, US); 100 ft., *Allen 5211* (US); Osa Peninsula, Corcovado National Park, 0–1 km W of park headquarters at Sirena, 0–200 m, *Gentry & Acevedo 48690* (B, CM, MO), *Knapp 2192* (MO, PMA), *Liesner 2846* (MO), *2996* (MO); Parque Nacional Corcovado, 0–150 m, 8°27–30′N, 83°33–38′W, *Kernan 70* (CR, F, K, MO); Rincon de Osa, 20–300 m, *Liesner 1934* (MO); 5 km W of Rincon de Osa, NW of airfield, 50–200 m, 8°42′N, 83°31′W, *Burger & Liesner 7286* (MO, NY); E base of Fila Barrigones, 1 km S and 2 km W of Cañasas, 12 km S of Rincon de Osa, 60 m, 8°34′N, 83°25′W, *Croat & Grayum 59823* (MO); Las Cruces Botanical Garden, *Croat 57240* (MO). SAN JOSÉ: Santa María de Dota, *Croat 55204* (MO); Cerro Pelón, N base, just E of main road, 0.5 km S of San Martín de Puriscal, 800 m, 9°44′N, 84°23′W, *Grayum & Baker 4694* (MO); Montañas Jamaica, 2.5 km NE of Bijagual de Turrubares, Carara Reserve, 460–520 m, 9°45′N, 84°33.5′W, *Grayum et al. 5478* (MO); Río Negro, ca. 1.5 km E of Santa Rosa de Puriscal, 320 m, 9°42′N, 84°23′W, *Grayum et al. 8339* (CR, MO).

Anthurium fasciale Sodiro, Anales Univ. Centr. Ecuador 19: 288. 1905. TYPE: Ecuador. Tungurahua: Río Pastaza, *Sodiro s.n.* (holotype, B; isotype, G). Figures 126, 133.

Epiphytic or terrestrial; stem climbing, to 50 cm long, 1–3 cm diam.; roots moderately few, descending, drying 2 mm diam.; cataphylls subcoriaceous, lanceolate, 14–24 cm long, acute at apex, drying whitish, straw-colored, persisting as a reticulum of fibers. *Leaves* mostly spreading; petioles 11–40(60) cm long, 5–11 mm diam.,

D-shaped, flattened or convex with an acute medial rib adaxially, the margins sharply raised, rounded abaxially; geniculum moderately thicker than petiole, 1–2 cm long; sheath 2–7 cm long; blades coriaceous, oblong-linear to broadly oblong, narrowly acute at apex, obtuse to shortly attenuate or narrowly acute at base, 47–120 cm long, 5–20 cm wide, broadest at or near the middle, the margins moderately to conspicuously undulate; upper surface weakly glossy to semiglossy, slightly quilted, dark green, lower surface semiglossy to glossy, slightly to moderately paler; both surfaces drying green to yellow-brown; midrib convexly raised, or sometimes acutely raised toward the apex above, paler than surface, acutely raised below; primary lateral veins 17–33 per side, departing midrib at 60–90° angle, slightly arcuate to the collective vein, convexly raised above, flat and darker than surface below, drying raised on both surfaces; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins moderately obscure above, darker than surface below, raised above and below when dried; reticulate veins obscure; collective vein arising from the base, equally as prominent as interprimary veins, (1)2–7 mm from margin. *Inflorescences* erect-spreading; peduncle 8–40(62) cm long, 2–8 mm diam., 0.6–2.3× as long as petioles, terete; spathe reflexed, subcoriaceous, green, ovate to broadly oblong, ca. 6.5–12 cm long, 1.5–3 cm wide, broadest in the lower half, the acumen inrolled, 4–8 mm long, acute to narrowly acute at base; spadix dark red, cylindroid to slightly tapered, sessile or stipitate to 5 mm, erect, straight or slightly curved, 5.5–12 cm long, 5–10 mm diam.; flowers (dried) rhombic, 1.6–1.7 mm long, 1.2–1.5 mm wide, the sides jaggedly sigmoid to straight; 8–11 flowers visible in principal spiral, 5–8 in alternate spiral; tepals semiglossy, minutely papillate, lateral tepals 0.7–0.8 mm wide, the inner margins erose, the outer margins 2–3-sided; pistils yellow-brown on drying, smooth, lacking raphide cells, rounded at apex, not at all protruding above the tepals; stigma linear, ca. 0.3 mm long; stamens emerging from near the middle, inclined over and obscuring pistil at anthesis, held against the pistil post anthesis; anthers 0.4–0.6 mm long, 0.4–0.5 mm wide; thecae obovoid-oblong, weakly divaricate. *Infructescence* erect to pendent; spathe persisting, green; spadix ca. (7.5)12–16 cm long, 1.5–2 cm diam.; berries red, obovoid, 7–8 mm long, 5 mm diam.; seeds 1–2 per berry, broadly oblong to rounded, flattened on one side, 4.4–5 mm long, 3–3.5 mm diam., 1.5–2 mm thick, with a transparent, gelatinous appendage at base and dark gelatinous appendage at apex.

A member of series *Multinervia*, *Anthurium fasciale* occurs in Morona–Santiago, Napo, Pastaza, and Tungurahua provinces in Ecuador, at 970–1,600 m in premontane moist and very wet premontane forest life zones.

This species is distinguished by its rather long cataphylls which quickly weather to pale fibers, its abaxially rounded and adaxially flattened or medially ribbed petioles with sharply raised margins, and its oblong leaf blades drying green or yellowish with the primary lateral veins rather numerous, but unequal in prominence and ascending at a broad angle from the midrib. Another distinctive feature is the dark red spadix with exserted stamens.

A collection which may belong here (*Croat 50586*), made from a cultivated plant reportedly collected south of Puyo on the road to Macas, differs in having stamens not exserted and a relatively shorter peduncle (0.4× as long as the petioles), but agrees well with *A. fasciale* in other characters, including pistil color (on drying).

The type specimen and another Sodiro collection closely resembling it are unusual in having peduncles 16–25 cm longer than any other specimens.

Anthurium fasciale is likely to be confused only with *A. penningtonii*, also from high elevations on the eastern slopes of the Andes and also a member of series *Multinervia*. *Anthurium penningtonii* differs in having more elliptic leaf blades with more numerous, sharply raised primary lateral veins, and a more slender spadix.

This species is also similar to *A. soukupii*, ranging from southern Ecuador to Bolivia. It shares similar leaf blades and a similar weakly tapered spadix. *Anthurium soukupii* occurs at a higher elevation (2,200 to 2,400 m) and also differs in having a more or less triangular petiole and fewer flowers per spiral (7 or less). In addition, the dark-drying pistils of that species are densely marked with raphide cells and have prominently exserted styles. In contrast, the pistils of *A. fasciale* dry yellow-brown, with no raphide cells visible and are broadly rounded at the apex with the stigmas not at all protruding.

ECUADOR: MORONA–SANTIAGO: Valle de Calagras, 11 km E of San Juan Bosco, Descanso, 1,600 m, 3°02′S, 78°21′W, *Dodson et al. 10495a* (SEL). NAPO: Holín–Loreto, Km 32, 8 km W of Guamaní, 1,200 m, 0°43′S, 77°38′W, *Neill et al. 8624* (MO). PASTAZA: cultivated S of Puyo, road to Macas, *Croat 50586* (MO, QCA); Río Negro, Baños, *Croat 50587* (MO, QCA); Puyo–Diez de Agosto and Arajuno, 8.2 km NE of Diez de Agosto, 970 m, 1°37′S, 77°51′W, *Croat 59017* (AAU, B, BM, CM, GH, K, M, MO, QCA, RSA, US); Puyo–Baños, 5.7 km W of Shell, 1,070 m, 1°26′S, 78°09′W, *Croat 59073* (MO, QCA); 2 km NE of Mera, Hacienda San Antonio

de Baron von Humboldt, 1,100 m, 1°27′S, 78°06′W, *Palacios et al. 58* (MO); Mera, *Lugo 25* (S); Río Pastaza, Mera, *Lugo 1117* (GB); El Topo, 1,250 m, 1°25′S, 78°10′W, *Harling 3403* (S). TUNGURAHUA: Río Pastaza (Río Chambo), *Sodiro s.n., 8/1904* (G), *Sodiro s.n., 12/1906* (B).

Anthurium fatoense K. Krause, Notizbl. Bot. Gart. Berlin–Dahlem 11: 611. 1932. TYPE: Panama. Colón: Dos Bocas, Río Fato Valley, 40–80 m, *Pittier 4227* (holotype, US). Figures 134–136.

Epiphytic; stem 10–60 cm long, 1–2 cm diam.; leaf scars obscured by root mass; roots dense, ascending to descending, numerous, pale green to white, smooth to very pubescent, short to elongate, usually tapered, 1–4 mm diam.; cataphylls subcoriaceous to coriaceous, oblong-lanceolate, 5–14.5 cm long, acute at apex with a subapical apiculum, pale yellow-green, sometimes tinged with red, drying medium brown, persisting semi-intact, soon deciduous. *Leaves* erect to spreading; petioles 2.5–9.5 cm long, 5–8 mm diam., sharply quadrangular to angularly D-shaped to occasionally subterete, flattened to broadly sulcate adaxially, sharply 1–3-ribbed or sometimes rounded abaxially, the surface minutely pale-speckled; geniculum paler and thicker than petiole, 0.7–1(2) cm long; blades subcoriaceous, oblong-oblanceolate to oblanceolate to oblong-ovate, long-acuminate at apex, acute to obtuse to narrowly rounded at base, 24–83 cm long, 6–26 cm wide, broadest at or above the middle, the margins weakly and broadly undulate; upper surface matte to glossy, medium green, lower surface semiglossy to glossy, paler, drying greenish to greenish brown; midrib flat at base, becoming sharply and narrowly raised toward the apex above, raised and sharply 2-ribbed or prominently convex-raised at base below, becoming convex to flat toward the apex; primary lateral veins 8–16 per side, departing midrib at 40–50° angle, arcuate-ascending, narrowly raised above, less so and darker than surface below; interprimary veins less conspicuous than primary lateral veins; tertiary veins obscure above, darker than surface below; collective vein arising from near the apex or absent, 2–9 mm from margin. *Inflorescence* erect-spreading to arching-pendent, shorter than or equaling leaves; peduncle 14–48 cm long, 2–6(9)× as long as petioles, green to reddish, weakly striate, terete to subterete, faintly ribbed; spathe spreading to reflexed, subcoriaceous, light green, sometimes tinged with purple, narrowly lanceolate, 5.5–9(13.5) cm long, 0.7–1.3(2) cm wide, broadest near base, inserted at 45–90° angle on peduncle, long-acuminate at apex (the acumen inrolled), obtuse to subcordate at base; spadix green to green tinged with red to pale reddish to reddish violet or purplish, oblong-cylindroid to long-tapered, 5–15 cm long, 4–10 mm diam. near base, 2.5–4 mm diam. near apex; flowers rhombic to weakly 4-lobed, 1.4–2.8 mm long, 1.8–3 mm wide, the sides smooth to jaggedly sigmoid; 5–9 flowers visible in principal spiral, 5–12 in alternate spiral; tepals matte to weakly glossy, minutely and densely papillate and pale punctate; lateral tepals 1.2–1.5 mm wide, the inner margins straight to broadly convex, somewhat erose, the outer margins 2–4-sided; pistils prominently to weakly raised, weakly glossy, papillate, green to white; stigma 0.4–0.5 mm long, brushlike; stamens emerging in slow progression from the base in a complete sequence, the laterals preceding the alternates by 6–34 spirals, the 3rd stamen preceding the 4th by 1–12 spirals, arranged in a circle around pistil; filaments translucent, 0.5 mm long, 0.4 mm wide; anthers yellow to white, 0.5–0.6 mm long, 0.5–0.8 mm wide; thecae broadly to oblong-ovoid, not divaricate; pollen yellow fading to white, sweet-scented. *Infructescence* spreading; spadix to 26 cm long, with berries scattered throughout; berries cream to greenish yellow or pale orange, oblong-ovoid to ovoid-ellipsoid, acute at apex, 4–7.8 mm long, 3.3–4.2 mm diam.; pericarp thickened; seeds 2 per berry, pale yellow with numerous pale, granular raphide cells on the surface, oblong-ovoid, slightly or not at all flattened, 2.6–3 mm long, 1.5–1.8 mm diam., 1–1.3 mm thick, with a transparent, gelatinous, sticky appendage.

Anthurium fatoense is known from southern Costa Rica and Panama, occurring principally on the Caribbean slope in wetter parts of tropical moist forest, as well as in tropical wet, premontane wet, and lower montane wet forest, from sea level to nearly 1,200 m. It also occurs on the Pacific slope in the Fortuna area of Chiriquí Province in Panama.

Anthurium fatoense is considerably variable in size of the leaves and inflorescences as well as in berry color. It is distinguished by its slender, erect, pointed roots, short, conspicuously sheathed petioles, green-drying blades, and its tapered, greenish spadix with the stamens closely clustered over the pistil, the latter being not at all apparent.

This species is most easly confused with *A. consobrinum*, but that species has prominently emergent pistils that emerge well ahead of the stamens and extend several millimeters above the stamens.

COSTA RICA: ALAJUELA: Naranjo–Aguas Zarcas, 8.5 km NE of Villa Quesada Hwy. 15, 600 m, *Croat 46976* (MO); 2 km N of Santa Rosa, 15 km N of Boca Arenal on Quesada–Muelle San Carlos–Los Chiles road, 100 m, 10°38′N, 84°31′W, *Liesner et al. 15024* (MO). CARTAGO: cultivated, *Madison 6957* (MO, SEL). LIMÓN: 7 km W of Bribrí, 100–250 m, *Gomez et al. 20386* (CR, MO); 10 mi. S of Punta Cahuita, 3 mi. S of turnoff to Bribrí, 70 m, *Croat 43197* (MO); Cantón de Talamanca, Suretka, 9°34′N, 82°56′W, *Barringer et al. 3554* (MO); Caribbean Coast, between Río Bananito and Cahuita, 0–10 m, 9°53′N, 82°59′W, *Burger et al. 10485* (MO); Refugio Gandoca–Manzanillo, 0–5 m, 9°36′N, 82°36′W, *Grayum 8018* (MO); Hitoy Cerere reserve, Río Cerere, SW of Valle La Estrella, 1 km upstream from Quebrada Barrera, 90–200 m, 9°40.5′N, 83°02′W, *Grayum & Hammel 5787* (MO); Río Sizaola, between Limón and Shiroles, 6.5 mi. SW of Bribrí, 6 mi. SW of Bambú, 50 m, *Croat 43295* (MO). PUNTARENAS: Cantón de Coto Brus, 6 km W of San Vito de Java, 1,200 m, 8°49′N, 82°58′W, cultivated at Las Cruces Tropical Botanical Garden, *Croat 57229* (CR, MO). PANAMA: BOCAS DEL TORO: 15 km S of Changuinola, 300–500 m, *Antonio 3147* (MO); Cerro Banyic, above Quebrada Huron, 170–400 m, *Kirkbride & Duke 606* (MO); Fortuna Road, Changuinola–Luzon, *Kennedy 3266* (F, MO); Fortuna Lake--Chiriquí Grande, 1.2–8 km N of Continental Divide, 310–1,000 m, *Churchill et al. 4635, 4942* (MO), *Croat & Grayum 60121* (K, MO, RSA), *60171* (CM, MO), *60256* (MO, RSA), *60423* (B, K, MO, RSA, US), *Hampshire & Whitefoord 484* (BM); along road from Fortuna Dam toward Chiriquí Grande, 10 mi. from Continental Divide, 120 m, 8°55′N, 82°10′W, *McPherson 8587* (MO); Río Guarumo, Chiriquicito to 5 mi. S along Río Guarumo, *Lewis et al. 2051* (MO); Chiriquí Lagoon, Fish Creek Mts., *von Wedel 2350* (MO). CHIRIQUÍ: Fortuna Road, E of Fortuna, 1,200–1,600 m, *Folsom et al. 5293* (MO); between Gualaca and Fortuna Dam site, 5.9–11.8 mi. N of Los Planes de Hornito, 1,100–1,470 m, *Antonio 5175* (MO), *Croat 48705* (MO, F, DUKE, NY, RSA, S, US), *48716* (FTG, MO), *50095* (F, MO, TEX, W), *49893* (FTG, MISSA, MO), *Knapp & Vodicka 5517* (MO); vic. Fortuna Dam, N of the lake, 1,100 m, *McPherson 10407* (MO); along trail from Forestry Nursery to Río Hornito, 1,100–1,200 m, 8°45′N, 82°15′W, *Thompson 5029* (CM). COCLÉ: Cerro Tute, *Antonio 2055* (MO); Llano Grande–Coclecito, vic. Continental Divide, 400–600 m, *Antonio 1358, 3598* (MO), *Croat 49220* (MO), *D'Arcy & Sytsma 14690* (MO), *Hammel 1619* (MO), *3483* (MO, SEL), *Sytsma 3880* (MO, PMA); S of Cascajal, Continental Divide, 800–900 m, 8°45′N, 80°25′W, *Knapp 1961* (MO); 9–12 mi. from Llano Grande, 170–330 m, *Churchill et al. 3994, 4165* (MO), *Hammel 1808, 1908* (MO); El Copé Region, Alto Calvario, 600–800 m, *Folsom 3183* (MO); El Copé W of sawmill, *Hammel 2420, 2441* (MO); Continental Divide, sawmill above El Copé, 750–800 m, 8°40′N, 80°36′W, *Knapp & Dressler 3501* (B, MO); El Valle Region, El Valle de Antón, 2 km W of Cerro Pilón, vic. La Mesa, 860–900 m, *Croat 37347* (MO, SEL); El Valle de Antón, N of Cerro Gaital, vic. La Mesa, 700 m, *Hammel 3902* (MO). COLÓN: San Lucas, 100 m, *Hammel 4549* (MO); Cerro Bruja, S slope, Río Escandaloso, 200 m, *Hammel 3197* (MO); Portobelo Region, Río Escandaloso, abandoned Manganese mine, 170 m, *Hammel 2661* (MO, SEL); Río Cascajal, *Croat 33649* (MO, PMA); Río Guanche, E of Colón, W of Portobelo, 50 m, 9°30′N, 79°40′W, *McPherson 8513* (MO); Río Boqueron headwaters, fork with Río Nombre de Diosito, 170 m, *Hammel 3947* (MO); Río Tato, Dos Bocas, 40–80 m, *Pittier 4227* (US). VERAGUAS: trail from Barrera to gold mine "Cocuyo," 30–200 m, *Hammel 5192* (MO). Santa Fe Region, Cerro Tute, beyond Escuela Agrícola Alto Piedra, NW of Santa Fe, 900–1,250 m, *Antonio 2910, 4039* (MO), *Croat 48940* (MO), *Sytsma & Antonio 3049* (MO), *3068* (K, MO), *Sytsma & Andersson 4658* (MO); between Escuela Agrícola Alto Piedra and Río Dos Bocas, 350–770 m, *Croat 25941* (MO), *27365* (MO), *27583* (MO), *27749* (MO); 5.9 mi. N of Escuela Circlo Alto de Piedra, between Santa Fe and Río San Luis, 480 m, *Croat 66940* (MO); Río Primero Brazo, 5 mi. NW of Santa Fe, 700–1,200 m, *Croat 23115* (MO); 3.9–5 mi. N of Santa Fe, 500–1,000 m, *Folsom 2949* (MO, PMA), *Gentry 2953* (MO); 1–3 km N of Escuela Agrícola Alto de Piedra, N of Santa Fe, 900–1,250 m, *Mori & Kallunki 2560* (MO); 6–7 km W of Santa Fe, 970 m, *Nee 9807* (MO), *Nee 11220* (MO, PMA); between Santa Fe and Río Calovébora, 735 m, *Croat & Folsom 34124* (B, CAS, COL, CR, DUKE, F, MBM, MEXU, MO, NY, PMA, RSA, US), *Knapp & Sytsma 2623* (MO), *Hamilton & Krager 3965* (MO).

Anthurium fendleri Schott, Prodr. 468. 1860. TYPE: Venezuela. Colonia Tovar, *Fendler 1343* (lectotype, K; isolectotype, GH). Figures 137–139.

Anthurium recusatum Schott, Prodr. 467. 1860. TYPE: cultivated plant of unknown origin, illustrated by Schott, Aroideae 525–527, serves as the type.

Anthurium buenaventurae Engl., Bot. Jahrb. Syst. 25: 363. 1898. TYPE: Colombia. Valle: near Buenaventura, vic. Las Juntas near Dagua, 200–600 m, *Lehmann 5332* (holotype, B; isotype, F).

Anthurium canasas Croat, Aroideana 2(1): 30. 1979. TYPE: Panama. Veraguas: Dist. Cañasas, ca. 1 km above Cañasas on road to Los Valles, 230 m, *Croat 37051* (holotype, MO; isotypes, B, COL, F, PMA, S, SCZ, US).

Epilithic, epiphytic or terrestrial, on steep rocky banks; stem to 15 cm long, 1–3 cm diam.; roots moderately numerous, descending, greenish to brownish, densely pubescent, moderately elongate, tapered, 2–5 mm diam.; cataphylls moderately thin, broadly lanceolate, 5–10 cm long, acute with subapical apiculum at apex, yellowish red, heavily pale-speckled, drying brown, persisting semi-intact to fibrous, eventually deciduous. *Leaves* erect-spreading; petioles (2)4–47 cm long, 5–8 mm diam., D-shaped to subtriangular, narrowly to broadly sulcate adaxially, the margins sharply to bluntly raised, rounded to 1–5-ribbed abaxially, the surface medium green, pale-speckled; geniculum thicker and paler than petiole, becoming fissured transversely with age, (0.5)1–2.5 cm long; blades chartaceous to subcoriaceous, oblanceolate to broadly elliptic, gradually acuminate at apex, usually rounded or shallowly cordate, sometimes acute to obtuse at

base, (15)30–81 cm long, (6)10–34 cm wide, broadest just above the middle, the margins broadly undulate; upper surface semiglossy, dark to medium green, lower surface weakly glossy to semiglossy, slightly paler; midrib flat at base, becoming convexly raised toward the apex above, slightly paler than surface, prominently higher than broad and acutely angular at base below, becoming convexly raised toward the apex; primary lateral veins 8–12 per side, arcuate-ascending, the lowermost free to the margin, loop-connecting to the collective vein in apical third, convexly raised, sometimes sunken in grooves above, prominently convex below; tertiary veins sunken above, raised and darker than surface below; reticulate veins obscure above, weakly visible below; collective vein arising from about the middle of the blade, sunken above, raised below, slightly less prominent than primary lateral veins, 4–12 mm from margin. *Inflorescences* spreading or stiffly erect; peduncle 30–79.5 cm long, 1.6–3.8× as long as petiole, terete or weakly to prominently ribbed abaxially, sometimes also adaxially; spathe spreading and recurving or loosely coiled, caducous, thin, soon drying and weathering, green or green tinged with violet-purple (B & K purple 5/10), linear-lanceolate to narrowly triangular, 5.5–11.5 cm long, 0.9–2 cm wide, broadest near the base, inserted at 60–80° angle on peduncle, narrowly acuminate at apex, acute at base, the margins meeting at 40–50° angle; stipe green, 6–18 mm long; spadix maroon (B & K red-purple 2/10), long-tapered, 7.5–21 cm long, 4–7 mm diam. near base, 2.5–4 mm diam. near apex; flowers square to rhombic, 2.5–3 mm in both directions, the sides smoothly to jaggedly sigmoid; 4–8 flowers visible in principal spiral, 5–10 in alternate spiral; tepals matte, weakly punctate, densely and minutely papillate; lateral tepals 1.3–1.8 mm wide, the inner margins broadly convex, the outer margins 2–3-sided; pistils early emergent, 0.1–0.2 mm, green becoming violet-purple, sometimes green with violet-purple splotches; stigma ellipsoid, light purple-violet, 0.6 mm long, dry and full of slightly exserted bristles at anthesis, becoming dark and caviform, droplets conspicuous, appearing 2–4 days before stamens emerge; stamens emerging in a slow progression from the base, the laterals preceding the alternates by 3–5 spirals, the 3rd stamen preceding the 4th by 1–3 spirals, held just above tepals; anthers creamy to yellow, 0.4–0.5 mm long, 0.8–0.9 mm wide; thecae ovoid, not divaricate; pollen bright to pale yellow, soon fading to white. *Infructescence* pendent; berries violet-purple, obovoid, rounded at apex, 6.7–7 mm long; mesocarp thick, gelatinous, white; seeds 1–2 per berry, purplish, 4.5–5 mm long, 2–3.5 mm diam., 0.7–2 mm thick.

Anthurium fendleri ranges from sea level to usually less than 1,000 m, less frequently to 2,430 m, generally in partially shaded areas, in tropical dry, tropical moist, premontane wet, and premontane dry (presumably in premontane moist as well) forest life zones in Venezuela and Colombia. In Panama, it is rare and occurs in tropical moist forest.

Anthurium fendleri was previously known only from the Cordillera de La Costa of Venezuela west of Caracas, but is now known to range throughout most of western Colombia into the Serranía de Perijá in northeastern Colombia and western Venezuela, along the Río Meta in the state of Apure and southward along the eastern edge of the Andes to the Departments of Meta and Vichada, in southwestern Colombia. Disjunct populations include those in the Chocó, Colombia, in the Serranía del Darién, Panama, and in central Panama on the Pacific slope near Cañasas in Veraguas Province. Apart from *A. jenmanii*, *A. fendleri* appears to be the only species of sect. *Pachyneurium* that ranges from northern South America (well outside the Amazon Basin) to lowland Amazonia. While *A. jenmanii* achieves this by wrapping around the Guianas and into Amapá, Brazil, *A. fendleri* ranges south through Colombia, as outlined above.

This species differs from most members of the section by virtue of its thinner leaves and dark purple berries, and sometimes markedly rounded to subcordate leaf bases. It is further distinguished by its rich green, oblanceolate-elliptic to broadly elliptic leaves, which dry more or less olive-green and bicolorous, by its sunken tertiary veins, its ribbed petioles, thin, caducous spathe, slender reddish brown spadix, and violet-purple berries.

Anthurium fendleri is apparently most closely related to *A. bonplandii*, and some Colombian material may be confused with that species. *Anthurium bonplandii* differs in having leaves that dry brown and are usually conspicuously dark-glandular punctate and/or pustular (especially below) and acute at the base.

This species is variable in leaf size and shape and the base may vary from nearly acute to subcordate. Specimens from Apure in Venezuela seem to have somewhat more coriaceous leaf blades. *Croat 56578*, collected on rocky cliffs near the Río Claro in Antioquia, Colombia, has unusually coriaceous leaf blades. Another aberrant collection is *Stergios et al. 4568*, from Portuguesa, Venezuela, in Municipio de Ospino; it has leaf blades

which are more coriaceous and less concolorous than usual, and obtuse-cuneate at the base. Other collections from the same area are from lower elevations, and have leaf blades that are more typically thinly coriaceous and bicolorous on drying, and conspicuously shallowly cordate at the base.

Though *A. recusatum* Schott was described from a cultivated plant of unknown origin, the Schott illustrations show it to be remarkably similar to *A. fendleri*, and it is here considered synonymous.

COLOMBIA. Río Magdalena, *Von Bayern 44* (BOG). ANTIOQUIA: Mpo. San Luis, Puerto Triunfo–Medellin; Río Claro, 51°54′N, 74°51′W, *Croat 56578* (CM, COL, DUKE, GH, INPA, JAUM, MO, MY, NY, P, PMA, QCA, SEL, US, VEN); N section of cañón of Río Claro, 325 m, 5°53′N, 74°39′W, *Cogollo 1342* (COL, MO); central section of canyon, 350–475 m, *Cogollo 615* (COL, MO), *1302* (COL, MO); Dabeiba, 1,350 m, *Backley & Gutierrez 1822* (COL). ATLÁNTICO: Barranquilla, *Elias 1477* (F); Sabana Larga, SSW of Barranquila, *Elias 1296* (COL, F, GH, US). BOLÍVAR: Juan Arias–San Pedro, *Castenada 9855* (COL). BOYACÁ: Río Casanare, Esmeralda, 130 m, *Cuatrecasas 3818* (US); CÉSAR: Río Magdalena, above Cañasas on road to Los Valles, Rincón Hondo, *Allen 285* (MO). CHOCÓ: Serranía del Darién, W of Unguia, Río Tigre Base Camp, 300 m, *Gentry & Aguirre 15232* (MO, COL); Acandí, Bahía Zardí, 0–5 m, 8°24′N, 77°07′W, *Betancur et al. 1249* (MO). CUNDINAMARCA: Cascajal–Tabla Grande, Nocaima Region, 1,000 m, *Plowman et al. 5246* (COL). GUAJIRA: Sierra de San Antonio, Cuchilla de La Nueva, 300 m, 11°05′N, 73°30′W, *Cuadros & Gentry 2962* (MO). MAGDALENA: Río Frío–San Andrés de La Sierra, El Platanal, *Pittier 1697* (US); Santa Marta, 1,500 m, *Smith et al. 2305* (K), *2309* (BM, F, GH, MO, NY, US). META: 310 m, 2°96′N, 73°10′W, *Madison 1224* (GH); Villavicencio–Granada, N of Granada, 520 m, *Croat 55519* (MO); central mountains, Approach Ridge, 1,100 m, *Philipson & Idrobo 1900* (COL); Sierra de La Macarena, N escarpment, 800 m, *Philipson 2312* (COL); 850 m, *Idrobo 4866* (COL); NE end, Hda. Los Micos, Quebrada Honda, 460 m, *Plowman et al. 4210* (GJ, US). SAN ANTONIO: Sierra de Santa Marta, 1,000 m, Hanbury-Tracy 449 (K). SANTANDER: Río Surata Valley, Bucaramanga, 400–600 m, *Killip & Smith 16234* (GH, NY, US). SANTANDER SUR: Bucaramanga–Zapatoca, 5 km S of Girón, 660 m, 7°03′N, 73°12′W, *Croat 56545* (AAU, B, CAS, CM, COL, DUKE, K, M, MO, NY, RSA, SAR, SEL, UCLA, US); Río Carare–Río Magdalena, Puerto Berrio, 100–700 m, *Haught 1710* (US); Mpo. Florida Blanca, Verada Los Cauchos, S of Bucaramanga, 1,000 m, 7°01′N, 73°05′W, *Croat 56388* (CM, COL, K, L, MBM, MO, SAR, SEL, US, W). VALLE: Buenaventura, Las Juntas and Dagua, 200–600 m, *Lehmann 5332* (B, F); Cali–Buenaventura, Quebrada La Guinea, 1.2 km E of Cisneros, 220–260 m, 3°47′N, 76°46′W, *Croat 62821* (FT, IBE, MO); Río Dagua–Pepita, 302 m, *André 373* (K); Cordillera Occidental, La Cumbre, 1,700–2,100 m, *Pennell & Killip 5756* (NY). VICHADA: Cerro Rocoso, Territorio Faunístico del Tauparro, 100 m, *Vincelli 1201* (MO). PANAMA: VERAGUAS: above Cañasas on road to Los Valles, *Croat 37051* (B, CM, COL, DUKE, ENCB, F, K, KYO, MEXU, MO, NY, PMA, QCA, RSA, S, SAR, SCZ, TEX, VEN, US). VENEZUELA: Cultivated at Jardín Botánico de Ciudad Univ., *Braun 2* (VEN). APURE: Distrito Achaguas–Rómulo Gallegos, Río Capanaparo, Hato San Joaquin, 100 m, 6°48–52′N, 68°45–48′W, *Gragson & Gragson 92* (US). ARAGUA: Colonia Tovar, *Fendler 1341, 1343, 1344* (GH); Corgua, El Agricultor, *Trujillo 3833* (MY); Maracay, *Trujillo 4889* (MY), *Vogel 1175* (M); 500 m, *Bunting 2022C, 2022A* (NY); Parque Nacional Henri Pittier, 500–600 m, *Bunting 4788* (NY); Pozo del Diablo, *Fernández 270* (MY); Maracay–Ocumare, near Rancho Grande, 1,200 m, *Bunting 3393A* (NY). BARINAS: rd. to Barinas, NE of Santa Bárbara, 200 m, *Gentry & Puig-Ross 14271* (MO); Barinas–Mérida, N of Barinitas, along Hwy. 1, 450 m, *Croat 54754* (MO, VEN); between Barinitas–Altamira road and Calderas, 800 m, *Bunting 2263* (MY, NY). COJEDES: Ditto. El Limero, N of Tinaco, 100 m, *Delascio 4187* (VEN). FALCÓN: 440–1,200 m, *Liesner et al. 8283* (VEN). FALCÓN–LARA: Cerro Socopo, 500–1,000 m, *Liesner et al. 8432* (MO, NY, VEN), *8441* (MO, VEN). GUÁRICO: N of San Juan de los Morros at La Puerta, 380 m, *Bunting 2208* (NY). LARA: Dtto. Jiménez, Paso de Angosturo, 500 m, *Steyermark & Espinoza 107627* (MO, VEN); Dtto. Palavencino, Valle de el Altar, 250 m, *Steyermark et al. 109917* (F, VEN). MÉRIDA: Beguilla–Mucuchachi, 1,065–2,430 m, *Steyermark 56316* (F); El Vigia–Tovar, N of Santa Cruz de Mora, 450 m, *Croat 54878* (B, MO); Mérida–El Vigia, 650–850 m, *Bunting 2309A* (MY), *2744* (MY, NY), *2792* (MY); Río Caparo, ESE of Santa Bárbara, 100–250 m, *Liesner & González 9281* (MO). PORTUGUESA: ENE of Agua Blanca, NE Of Acrigua, 190 m, *Steyermark & Rabe 96474* (MO, VEN); NNE of Guanare, 1,450–1,520 m, *Steyermark et al. 126795* (MO, VEN); NE of Boca de Monte, NNE of Guanare, 400–500 m, *Steyermark et al. 127104* (MO, VEN). Río Saguas, border of Trujillo, El Amparo, 800–850 m, *Bunting 2294* (MY); Río Tucupido, S of Dam, WSW of Guanare by air, 100–200 m, *Liesner & González 12544, 12554* (MO); Dtto, Guanare, UNELLEZ property, 9°04′N, 69°49′W, *Aymard 1306* (MO); Mpo. Ospino, La Estación, 800–1,200 m, 9°25–27′N, 69°30–31′W, *Stergios et al. 4568* (MO). TACHIRÁ: La Fría–La Grita, 200–250 m, *Bunting 2487, 2508* (MY); Lobatera–Ureña, 1,216–1,250 m, *Bunting 2350* (MY); 13 km NW of Lobatera, *Bunting 2349* (NY); vic. San Cristóbal, 1,000 m, *Bunting 4369* (MO, NY); 925 m, *Bunting 4837* (NY); San Cristóbal–Barinas, 60 km E of San Cristóbal, 460 m, *Bunting 13020* (NY); San Cristóbal–Santo Domingo, 250–350 m, *Bunting 2384A, 2398* (MY, NY); 250 m, *Bunting 2399* (NY); 300–350 m, *Bunting 2384B* (NY); E of Ayari, 250 m, *Steyermark & Rabe 96659* (MO, VEN), *Steyermark et al. 119464* (MO, VEN); Río Frío, Junction of Río Quinimari–Río Frío, 480–500 m, *Steyermark & Liesner 119115* (MO, VEN); Río Negro, 450 m, *Liesner & Guarigila 11835* (MO, VEN); Sierra el Casadero, Las Dantas–Las Adjuntas, 850 m, *Steyermark et al. 120173* (B, CM, K, MO, VEN). TRUJILLO: Sabana de Mendoza–Valera, *Bunting 2825* (MY); Valera, *Pittier 10793* (US); 20 km NE of Agua Viva, E of Valerita, 150 m, *Bunting 2817* (NY). YARACUY: E of Salóm, W of Valencia, NE of Nirgua, 790 m, *Croat 54612* (BM, K, MO, VEN). ZULIA: Serranía de Perijá, Río Palmar, 450 m, *Chitty & Benkowski 3090* (VEN); Dtto. Bolívar, Piedras Blancas–El Río Chiquio, W of Embalse, 6.5 km N of Piedras Blancas, 75–125 m, *Bunting & Alfonso 8029* (NY); 20–25 km W of La Villa, 225–350 m, *Bunting et al.*

8799 (NY); Dtto. Colón, Casigua el Cubo, 150 m, *Bunting et al. 7241* (NY); on the outskirts of Casigua El Cubo, sector Los Manuels, 7–14 km N of Casigua, *Bunting et al. 7377* (NY); Dtto. Lagunillas, Serranía de Ziruma–El Empalado, 13 km N of Embalse, 550–600 m, *Bunting et al. 11279* (NY); Dtto. Mara, 400–530 m, *Steyermark et al. 122687A* (MO).

Anthurium galactospadix Croat, sp. nov. TYPE: Brazil. Acre: N bank of Rio Juruá, opposite Cruzeiro do Sul, *Prance et al. 2924* (holotype, INPA; isotypes, NY, US). Figures 140, 143, 193, 343, 344.

Planta epiphytica; internodia brevia, 2–3 cm diam.; cataphyllum lanceolatum, persistens semi-intactum; petiolus 11.5–28 cm longus, 5–10 mm diam., adaxile uninervis, abaxile rotundatus vel trinervis; lamina late oblanceato-elliptica, 51–92 cm longa, 18–34 cm lata; nervis primariis lateralis 7–14 utroque. Pedunculus (4)6–11 cm longus, 3.5–5 mm diam., 0.4–0.7-plo longiores quam petiolo; spatha late lanceolato-elliptica, (4.5)5.5–12 cm longa, 1.5–3.5 cm lata, viridis; spadix leviter contractus, 7.5–11 cm longus, 8–14 mm diam., eburnius. Baccae ignotae.

Epiphytic; stem 2–3 cm diam.; roots dense, short, 3–5 mm diam.; cataphylls coriaceous, lanceolate, 7–9 cm long, acute to emarginate at apex, drying reddish brown, persisting semi-intact as a reticulum of fibers, splitting at apex. *Leaves* erect-spreading; petioles 11.5–28 cm long, 5–10 mm diam., D-shaped, with a prominent medial rib and sharply raised margins adaxially, rounded to 3-ribbed abaxially; geniculum shaped like and slightly thicker than petiole, 0.5–2 cm long; sheath 2.5–6.5 cm long; blades coriaceous to subcoriaceous, broadly oblanceolate-elliptic, acute to acuminate at apex, often attenuate with concave margins to long-acute to obtuse at base, 51–92 cm long, 18–34 cm wide, broadest above the middle, the margins moderately to strongly undulate; midrib sharply raised above, 3-ribbed near the base, becoming obtuse to acute below; primary lateral veins 7–14 per side, departing midrib at 40–50° angle, ascending straight or arcuate to the margin, acutely raised above, convexly raised below; interprimary veins absent except toward base and apex; tertiary veins obscure above, flat and darker than surface below, prominulous on both surfaces on drying; reticulate veins obscure; collective vein absent. *Inflorescences* erect; peduncle (4)6–11 cm long, 3.5–5 mm diam., 0.4–0.7× as long as petiole, terete; spathe usually erect to erect-spreading, sometimes reflexed, coriaceous, dark green to greenish white, broadly lanceolate-elliptic, flattened to navicular, (4.5)5.5–12 cm long, 1.5–3.5 cm wide, broadest at or near the middle, obtuse at apex (the acumen apiculate), acute at base, sometimes decurrent for up to ca. 1 cm; spadix pale green to creamy white, sessile, scarcely tapered, erect, slightly curved, (4)7.5–11 cm long, 8–14 mm diam. midway, 7–8 mm diam. near apex; flowers square, 1.1–1.9 mm long, 1.1–1.8 mm wide, the sides mostly straight parallel to spirals, jaggedly sigmoid perpendicular to spirals; 13–25 flowers visible in principal spiral, 15–28 in alternate spiral; tepals matte, smooth or covered with a waxy layer or minutely papillate; lateral tepals 0.5–0.8 mm, the inner margins rounded, weakly turned up against the pistil, the outer margins 2-sided; pistils emergent before stamens appear, square, ca. 1 mm in both directions, pale purplish lavender when fresh, colored ± like the tepals when dried; stigma 0.5 mm long, slitlike when young, becoming brushlike; stamens emerging somewhat sporadically from near the base, the laterals emerging to the apex before the first alternates appear, held erect on drying; anthers 0.4–0.6 mm long, 0.4–0.5 mm wide; thecae oblong-ellipsoid, not divaricate. *Infructescence* erect; spathe persisting; spadix (4)6–13 cm long, 0.8–1.7 cm diam.; mature fruits unknown.

Anthurium galactospadix is restricted to the western Amazon basin in "Trapecio Amazonico" in extreme southeastern Colombia, east-central Loreto near the Brazilian border in Peru, and in Acre and southern Amazonas in Brazil. It comprises epiphytes in tropical wet and tropical moist forest life zones (at least in Peru and Colombia), at 300 m or less.

This species is readily distinguished by its thick, relatively short, whitish spadix with the spathe usually longer than the spadix, its short peduncle, and its broadly elliptic-oblanceolate blades which are often attenuate with conspicuously concave margins toward the base. It is most closely related to *A. ernestii*, which differs in having usually thin, straw-colored cataphylls that perisist intact as fine reticulate fibers (vs. semi-intact with more coarse fibers), a shorter and narrower spathe and much less stout spadix which is variously colored but never whitish, and in usually having somewhat orange primary lateral veins upon drying (especially on the lower surface). In addition, the spadix of *A. ernestii* always surpasses the spathe, while in the present species it is shorter than the spathe. The specific epiphet for this species comes from "galacto-" (Greek), meaning milky white, alluding to the color of the spadix.

Two collections from Acre in Brazil (*Cid & Nelson 2563* and *Prance et al. 7471*) are ten-

tatively placed here. They differ in having a stem only 1–1.5 cm diam., leaf blades 43–76 cm long, and 11–20 cm wide, a peduncle 0.2–0.5× the length of the petiole, a spathe 4.5–6.5 cm long, 1.5–1.7 cm wide, and a spadix 3.1–5 cm long and 4–7 mm diam. In addition, the Prance et al. collection reports the spadix color as brown, and in the Cid & Nelson collection the peduncle equals the petiole in length. Another aberrant specimen is *Tessmann 5463*, from Yarina Cocha in Loreto, Peru, which has a more slender spadix and a spathe more than twice as long as the spadix. All of the above are probably aberrant specimens rather than representatives of distinct taxa.

BRAZIL: ACRE: Cruzeiro do Sul–Rio Branco, 44 km E of Cruzeiro do Sul, Fazenda da Dona Cabuca, 150 m, 7°38′S, 72°35′W, *Croat 62329* (INPA, MO); Sena Madureira–Rio Branco, Km 5.5, 140 m, 9°04′S, 68°39′W, *Croat & Rosas 62721* (CAS, IPA, K, MO, NY, US); Rio Acre, Seringal de São Francisco, *Ule 9206* (K, MG); Rio Moa, Cruzeiro do Sul, 150 m, 7°37′S, 72°37′W, *Croat & Rosas 62305* (AAU, F, INPA, MO); Mpo. Canamari Amazonas, Rio Jurua, opposite Cruzeiro do Sul, *Prance et al. 2924* (INPA, NY, US); 1 km upstream from Floresta, 150 m, 7°37′S, 72°36′W, *Croat 62533* (INPA, MO); Mpo. Cruzeiro do Sul, Cruzeiro do Sul–Rio Branco, vic. INCRA headquarters, 160 m, 7°38′S, 72°35′W, *Croat 62633* (INPA, MO); Mpo. Sena Madureira, Sena Madureira, *Cid & Nelson 2563* (INPA); Sena Madureira–Rio Branco, Km 7, *Prance et al. 7659* (NY, INPA); Mpo. Tarauaca, Tarauaca, 8°08′S, 70°50′W, *Prance et al. 7471* (NY, INPA, US). AMAZONAS: Mpo. Labrea, Rio Purus, 5 km above Labrea, *Prance et al. 8126* (NY, INPA). COLOMBIA: AMAZONAS: Río Loretoyacu: NW of Leticia, *Schultes & Black 8527* (COL, US). PERU. LORETO: Yarina Cocha, Pucallpa, *Tessmann 5463* (NY); Prov. Coronel Portillo, Río Abujao, Caserío de J.C. Mariategui–Mejico, one hour by boat from Caserío de Abujao, 300 m, 8°15′S, 73°45′W, *Diaz et al. 753* (MO).

Anthurium glaucospadix Croat, sp. nov. TYPE: Colombia. Cundinamarca: along road between Tena and La Mesa, 6 km NE of La Mesa, 1,300 m, 4°39′N, 74°26′W, *Croat 55257* (holotype, MO 3033409; isotypes, B, CAS, COL, F, GH, K, MBM, NY, RSA, SEL, US; live at MO). Figures 141, 142, 144, 145, 151.

Planta terrestris aut epiphytica; internodia brevia, 3–5(6) cm diam.; cataphyllum lanceolatum aut late lanceolata; petiolus 4–26(63) cm longus, 4–13 mm diam., acute D-formatus vel C-formatus aut plus minusve subquadrangularis, adaxile complanatus aut sulcatus, abaxile rotundatus aut 3–5(8) costatus; lamina 30–110 cm longa, (8)15–38 cm lata, plerumque oblanceolata, apica plerumque rotundato; nervis primariis lateralibus (7)9–18 utroque; pedunculus 30–60(90) cm longus, 3–10 mm diam.; spatha oblongo-lanceolata, purpureo-violacea aut viridis, (6)10–32 cm longa, (1)2–3.5 cm lata; spadix glaucus, caeruleo-viridis, longus et graduatim contractus, (7.5)14–33 cm longus, 5–12 mm diam. Baccae rubrae, oblongae, apice quadrato.

Terrestrial or epiphytic; stem to ca. 30 cm long, 3–5(6) cm diam.; roots dense, ascending, grayish white to pale green, soft, fuzzy, heavily woolly-pubescent, short, tapered, less than 10 cm long, 3–6 mm diam.; cataphylls subcoriaceous, lanceolate to broadly lanceolate, 3–12 cm long, acute to prominently emarginate at apex, green tinged with red, drying tan to reddish brown, persisting as a reticulum of fibers. *Leaves* semi-erect to spreading, occasionally pendent; petioles 4–26(63) cm long, 4–13 mm diam., sharply D-shaped or C-shaped to ± quadrangular, flattened to sulcate, often with a medial rib adaxially, the margins acutely raised, rounded to 3–5(8)-ribbed abaxially, the surface short-lineate, sometimes pinkish at base; geniculum slightly paler and thicker than petiole, becoming minutely fissured and scurfy adaxially, 1–3.5 cm long; sheath 3–7 cm long; blades moderately coriaceous, mostly oblanceolate, sometimes elliptic or oblong-oblanceolate, mostly rounded or rounded-emarginate on larger leaves, acute to slightly acuminate on smaller leaves at apex (the acumen inrolled, apiculate, sometimes inequilateral, downturned), mostly attenuate or acute (rarely rounded to obtuse) at base, 30–126 cm long, (8)15–47 cm wide, broadest in upper third, the margins slightly to moderately undulate; upper surface glossy to semiglossy or weakly glossy, medium green or yellow-green, lower surface semiglossy or occasionally matte, slightly paler, sometimes weakly to conspicuously whitish glaucescent; midrib flat at base, becoming obtusely to acutely raised toward the apex above, prominently obtuse-raised to 3–6-ribbed at base, becoming prominently convex toward the apex below, paler than surface above and below; primary lateral veins (7)9–18 per side, departing midrib at (30)50–70(80)° angle, weakly arcuate-ascending to the margin, sometimes appearing sinuate, convexly raised above, prominently convexly raised below, paler than surface; interprimary veins few, scarcely visible, sunken above, weakly raised below; tertiary veins weakly sunken or weakly raised above, prominently raised below; collective vein arising from near the apex, occasionally in the lower third (especially in smaller plants), sunken above, raised below, 3–9 mm from margin. *Inflorescences* semi-erect to spreading or pendent, shorter than, or almost equaling leaves; peduncle 30–60(98) cm long, 3–10 mm diam., 2–7× as long as petioles, green weakly tinged with red, pale short-lineate, terete to subterete, occasionally ribbed abaxially; spathe spreading to re-

flexed, sometimes twisted, occasionally with prominently revolute margins, subcoriaceous, matte above and below, green to green heavily tinged with red or purple-violet (especially on adaxial surface), oblong-lanceolate to oblong-triangular, (6)10–32(55) cm long, (1)2–3.5(4.0) cm wide, broadest near the base, inserted at 20–35° angle on peduncle, long-acuminate to abruptly short-acuminate at apex (the acumen often inrolled, 15–20 mm long), acute or decurrent to 6.5 cm at base; stipe rarely to 14 mm; spadix glaucous, bluish green, sometimes weakly tinged with purple or yellow, very long-tapered, ± erect to pendent and curved upward, (7.5)14–33 cm long, 5–12 mm diam. near base, 3–4 mm diam. near apex, broadest at the base; flowers rhombic, (1.6)1.8–3 mm long, (1)1.4–2.6 mm wide, the sides straight to jaggedly sigmoid; (5)6–9 flowers visible in principal spiral, 8--13 in alternate spiral; tepals glaucous, matte, minutely papillate, with a few scattered droplets, lateral tepals 1–1.6 mm wide, the inner margins broadly convex to straight, the outer margins ± straight or bluntly angled to obtusely 3-sided; pistils emergent, papillate, matte, squarish, pale green; stigma ellipsoid becoming circular, 0.4–0.6 mm long; stamens emerging rapidly in a regular and complete sequence over a 5–6-day period, the laterals preceding the alternates by (3)10–14 spirals, the 3rd stamen preceding the 4th by 1–3 spirals, inclined over and obscuring pistil; anthers pale yellow, 0.2–0.8 (dried) to 1 (fresh) mm long, 0.4–0.9 mm wide when fresh; thecae oblong, not divaricate; pollen pale yellow fading to cream, sweetly scented like rotting fruit. *Infructescence* with spathe persisting; spadix 12–53 cm long, 1.5–3.5 cm diam.; berries reddish purple, obovoid to oblong, 7–12 mm long, 4–5.5 mm diam.; pericarp thin, with raphide cells; mesocarp gelatinous; seeds 1–2 per berry, oblong, 4–5 mm long, 1.6–2.2 mm diam., 1–1.2 mm thick, with a mucilaginous appendage.

Anthurium glaucospadix is endemic to Colombia in the departments of Risaralda, Santander, Santander Sur, Cundinamarca, Valle and Huila, from 500 to 2,100 m. The distribution is unusual in that it included both slopes of the Cordillera Occidental (but only an unusually dry region of the Pacific slope). *Anthurium glaucospadix* is terrestrial or epiphytic on dry, rocky, steep slopes, exposed areas and thickets or as an understory herb in disturbed forest in premontane moist and premontane wet forest life zones.

This species is recognized by its long-tapered, bluish green, glaucous spadix (hence the name), its distinctive, usually emarginate or apically rounded blade, and by its reddish purple fruits.

This species is most closely related to *A. caucavallense*, also from Colombia, which differs by having a nonglaucous spadix, hooked cataphylls, more acute blade apices and more broadly spreading primary lateral veins.

Worthy of mention is *Triana 683/1702*, a mixed collection, two sheets of which are mounted with the leaves of a dicotyledonous plant, apparently of the Lecythidaceae. Although this number was recorded as being from Cundimarca, *Triana 682* is from Pasto.

COLOMBIA. CUNDINAMARCA: Fusagasuga–Girardot, km 63, 7 km S of Fusagasuga, 1,520 m, 4°25′N, 74°25′W, *Croat 52000* (AAU, B, CAS, CM, COL, G, JAUM, K, M, MEXU, MO, NY, QCA, SAR, US), *55428* (K, MO, NY, US); Fusagasuga–Melgar, 4 km SW of Fusagasuga, 1,525 m, *Barclay et al. 3645* (US); Mosquera–La Mesa, km 32, Laguna Pedro Palo above Finca San José, 2,000–2,250 m, *Gentry & Fallen 17159* (COL, MO); Tena–La Mesa, 6 km NE of La Mesa, 1,300 m, 4°39′N, 74°26′W, *Croat 55257* (B, CAS, COL, CM, DUKE, ENCB, F, GH, K, MBM, MO, NY, OOM, QCA, RSA, SAR, SEL, TEX, VBD, US, Z); Anolaima, 1,800 m, *Daniel & Augusto 4567* (COL); 6 km from La Mesa, 1,470 m, *Forero & Garzón 307* (COL); Quebrada Blanca, Choachi–La Calera, 1,900 m, *Acosta-Arteaga 25* (COL, MO); Quebrada Cabaña, Tocaima–Pubenza, 380–600 m, *Killip et al. 38371* (COL, US); Río Bogotá, above Apulo (Rafael Reyes), 2,100 m, *Plowman & Davis 3760* (COL); Santandercito, bridge over river, 1,600 m, *Silva Mojica 404* (COL); Anapoima, WSW of Bogota, 2,000 m, *Triana 683/1702* (BM, COL, P, US); Mpo. Tena, Lago Pedro Palo, 3 km N of Tena, 2,080 m, *Fernández & Mora 1445* (COL). HUILA: Cordillera Oriental, E of Neiva, 1,300–1,800 m, *Rusby & Pennell 998* (NY); 0.5 km above Vegalarge, 1,300 m, *Croat 55274* (MO); San Augustín, 1,500 m, *Bogner 846* (cultivated) (K). META: Cordillera Oriental, *Dryander 2154* (US). PASTO: 2,200 m, *Triana 682* (US). RISARALDA: along road between Pueblo Rico and Istmina, 14 km NW of Pueblo Rico, 5°03′N, 76°00′W, 780 m, *Croat 70848* (MO). SANTANDER: 0.5 km S of Berveo, 15 km NW of Velez, 2,000–2,500 m, *Fassett 25107* (MO, US). SANTANDER SUR: Mpo. Florida, cultivated at Jardín Botánico "Eloy Venezuela," 880 m, 7°05′N, 73°07′W, *Croat 56546* (MO). VALLE: Buga–Buenaventura: near Lago Calima, 1,430 m, 3°54′N, 76°33′W, *Croat 56747* (COL, MO); Km 44, Vereda El Trapiche, 1,140 m, 3°48′N, 76°37′W, *Croat 56753* (CM, COL, JAUM, MO, QCA, U, US); Cali–Buenaventura, NW of Loboguerrero at km 58.8, W of Cali, 575 m, 3°42′N, 76°39′W, *Croat 57518A* (MO), *57519* (COL, F, JAUM, MO, P, QCA, US, WIS); Cisneros, 300–500 m, *Killip 35595* (COL, F, US); Dagua, 700–900 m, *Killip 5441* (GH, NY, US), *5442* (NY); 1,200 m, *Heredia & Alvaré 369* (MO); Mun. Restrepo, along Río Grande between Pavas and Restrepo, 1,000 m, *Ramos & Reyna 908* (CUVC, F, MO).

Anthurium guanchezii Bunting, Phytologia 60(5): 294–295, fig 3. 1986. TYPE: Vene-

zuela, Amazonas: Dpt. Atures, Caño Cabeza de Monteco, affluent of Río Autana, 110–120 m, 4°52′N, 67°27′W, *Guanchez & Melgueiro 3451* (holotype, VEN; isotype, VZM).

Terrestrial; internodes short, drying 2.5 cm diam.; cataphylls persisting semi-intact; petioles 30 cm long, sheathing 1.7 cm at the base, cross-sectional shape not known; geniculum 0.8–1 cm long, remote from the blade base by 4.5 cm; blades pergamentaceous to subcoriaceous, broadly ovate, gradually acuminate at apex (the acumen 25 mm long), weakly cordate at base, 33.5 cm long, 22.5 cm wide; sinus 1.8 cm deep; the lower surface brown-punctate; the lower naked portion of midrib subterete and narrowly sulcate; posterior rib naked 1.5–2 cm; primary lateral veins ca. 8 per side, slender, departing midrib at ca. 40° angle, the lower 2–3 pairs at broader angle, arcuate-ascending to the margin; collective vein lacking or arising only in the upper fourth of the blade. *Inflorescences* slightly longer than leaves; peduncle 58 cm long; spathe reflexed-recurved, narrowly ovate, 9 cm long, 2.5 cm wide, acuminate at apex, decurrent 1.2 cm at base; stipe 1.7 cm long in front, 4 mm long in back; spadix weakly tapered, 8.2 cm long (apex missing), 7 mm diam. at anthesis, to 1.1 cm diam. in pre-fruiting condition. *Infructescence* not known.

Anthurium guanchezii is endemic to Venezuela and known only from the type locality at 110 to 120 m in a region which lies near the boundary between the tropical moist forest and premontane wet forest life zones.

The description given here is based only on the original type description and the species is therefore imperfectly known. Still, there is little doubt that *A. guanchezii* is a member of sect. *Pachyneurium* and is probably most closely related to *A. iramirezae*, which is also glandular-punctate, but differs in lacking a remote geniculum and in having a cartilaginous rather than a subcoriceous blade with basal veins not naked at the sinus. In addition, *A. iramirezae* has a narrower spathe, a sessile spadix and occurs at 1,350 m on granite outcrops.

Anthurium guanchezii is also related to *A. bonplandii* because of its glandular-punctations. It is easily distinguished from any of the varieties of that species by its ovate blades with a remote geniculum. While some specimens of *A. bonplandii* subsp. *bonplandii* have a remote geniculum, none have such ovate blades.

VENEZUELA: AMAZONAS: Dept. Atures, Caño Cabeza de Manteco, affluent of Río Autana, "Manteco" rapids, 110–120 m, 4°52′N, 67°27′W, *Guanchez & Melgueiro 3451* (VEN, VZM).

Anthurium halmoorei Croat, Ann. Missouri Bot. Gard. 70(2): 301. 1983. TYPE: Mexico. Nayarit: along Hwy. 28 between Tepíc and Jalcocotán at Km 15.5, ca. 1,000 m, *Croat 45337* (holotype, MO 2690192-193; isotypes, CAS, K, MEXU, MICH, SEL). Figures 146, 147, 152.

Epiphytic or epilithic; stem 1.5–5 cm diam.; roots dense, spreading to descending, tan to greenish, smooth, short, and stubby, 7–10 mm diam.; cataphylls coriaceous, lanceolate, (5)17–23 cm long, acute and apiculate at apex, green, sometimes reddish, drying tan to brown, persisting with apex remaining intact, dilacerating at base. *Leaves* erect to spreading; petioles 15–26 cm long, 7–18 mm diam., D-shaped to thicker than broad, broadly sulcate adaxially with the margins sharply raised to obtuse, sharply 1-ribbed to obscurely 3-ribbed or rounded abaxially, the surface pale-speckled; geniculum paler and thicker than petiole, 1–2.5 cm long; blades coriaceous, oblanceolate to oblanceolate–elliptic, short-acuminate at apex (the acumen shortly apiculate), acute to attenuate at base, 32–108 cm long, 10–43 cm wide, broadest above the middle, the margins prominently undulate; upper surface semiglossy, medium green, lower surface semiglossy to matte, much paler; midrib flat to obtusely angular at base, becoming narrowly acute and then flat toward the apex above, prominently higher than broad and 1-ribbed at base, becoming convexly raised toward the apex; primary lateral veins 5–14 per side, departing midrib at 40–55° angle, straight then arcuate-ascending to the margin, convexly raised, much paler than surface above, prominently raised and paler than surface below; interprimary veins less conspicuously raised above, visible and flat below; tertiary veins obscure above, darker than surface below; collective vein arising from near the apex or absent, flat to weakly sunken above, weakly raised and darker than surface below, 6–11 mm from margin. *Inflorescences* spreading, shorter than leaves; peduncle 32–43 cm long, 9–10 mm diam., 2–2.5× as long as petiole, subterete, obscurely angled; spathe spreading, subcoriaceous, green, sometimes tinged with purple (B & K yellow-green 6/10), ovate to broadly ovate, 13–16 cm long, 6.2–9.7 cm wide, broadest near the base, inserted at 70° angle on peduncle, acuminate at apex, acute at base; spadix green, purple or green heavily tinged with purple (B & K red-purple 2/5), cylindroid,

9–21 cm long, 11–27 mm diam. near base, 5–7 mm diam. near apex; flowers 4-lobed, 2.4–2.8 mm long, 2.7–3.2 mm wide, the sides sigmoid; 8–14 flowers visible in principal spiral, 12–20 in alternate spiral; tepals matte, weakly punctate, minutely papillate; lateral tepals 1.5–1.8 mm wide, the inner margins convex; pistils slightly raised, green, tinged with purple in the area of stigma; stigma linear, 0.4–0.6 mm long, droplets appearing 4–5 days before stamens emerge; stamens emerging ± rapidly from the base, inclined over the pistil; filaments exserted, ca. 0.3 mm long, 0.8 mm wide; anthers orange; thecae ellipsoid, scarcely divaricate; pollen orange, fading to white (B & K yellow 7/2.5). *Infructescence* 20–23 cm long, 3 cm diam., pendent; spathe usually persisting, green; berries pale yellow, greenish at tip, irregularly obovoid, 12–15 mm long, 7–9 mm diam.; mesocarp fleshy, with numerous raphide cells; seeds 2 per berry, pale tan, subglobose, weakly flattened, 5–6.5 mm long, 3.5–4.1 mm diam., ca. 2.5 mm thick, with a sticky appendage at both ends.

Anthurium halmoorei is restricted to western Mexico in the states of Nayarit, Jalisco, and Michoacán in seasonally very dry forests from 450 m to 1,000 m. It usually occurs on rocks on very steep slopes in forested areas.

This species is characterized by its generally oblanceolate or oblanceolate-elliptic blades with usually free-ending primary lateral veins; by its petiole which is acute abaxially; and especially by its ovate to ovate-elliptic spathe, green to purplish spadix, and greenish yellow mature berries.

Anthurium halmoorei is most easily confused with *A. schlechtendalii* subsp. *jimenezii*, which differs in having the petiole subquadrangular and usually flat abaxially, and in having a lanceolate spathe and red berries at maturity. The latter taxon occurs only in Guerrero and southern Oaxaca.

MEXICO: MICHOACÁN: Aguililla, *McVaugh 24741* (MICH); Coalcomán de Matamoros, *Rzedowski 16707* (ENCB, MICH). NAYARIT: Tepic–Jalcocotán, at Km 15.5, Hwy. 28, 1,000 m, *Croat 45337* (CAS, F, K, MEXU, MICH, MO, SEL, WIS); E of Tepic–Navarrete road, Barranca, NW of Tepic, *Dressler 339* (MO, UC); Jalcocotán, *Gentry & Gilly 10734* (MEXU, US), *McVaugh 12140* (MICH), *Moore & Bunting 8692* (BH); 4 km SE of Pochotitán, 1,000 m, 21°37′N, 104°41′W, *Miller & Téllez 3163* (B, MO); Mirador El Águila, *McVaugh 15281* (MICH); NE of Santa María de Oro, *Feddema 703* (MICH); vic. Tepic, *Bates et al. 1554* (BH), *Dressler 1024* (UC), *Ferris 6816* (DS), *Lewis s.n.* (MICH). JALISCO: Mpo. Jalisco, El Tuito–Puerto Vallarta, *Anderson 6113* (ENCB, MICH); 3 mi. N of El Refilon on road to Tepic, *Norris & Taranto 12645* (CAS, MO); Autlán de Navarro, *McVaugh 10224* (MICH), *Wilbur 2289* (MICH); El Tuito–Puerto Vallarta, *Delgado 359* (MICH), *Hernández 2608* (MEXU); S of San Pedro, *Koeppen & Iltis 593* (BH); Talpa de Allende, *McVaugh 23408* (MICH).

Anthurium hammelii Croat, Monogr. Syst. Bot. Missouri Bot. Gard. 14: 109. 1986. TYPE: Panama. Bocas del Toro: 5 km ENE of Cerro Pate Macho, near Finca Serrano, NE of Boquete, 1,675 m, *Hammel 6160* (holotype, MO 2802252). Figures 148, 153.

Description based on dried material only. Epiphytic; stem 1 cm diam.; cataphylls subcoriaceous, 6 cm long, brown, persisting semi-intact; petioles 33–34 cm long, 4 mm diam., apparently subterete; geniculum 1 cm long; blades subcoriaceous, oblong to oblong-elliptic, acuminate at apex (the acumen flat, 15–20 mm long), obtuse at base, 30–31 cm long, 5.5–7 cm wide, broadest at or near middle, the margins weakly undulate; midrib convexly raised above, more prominently so below; primary lateral veins 9–11 per side, departing midrib at 60° angle, arcuate to the collective vein, raised above and below; interprimary veins few, almost as conspicuous as primary lateral veins; tertiary veins prominulous above and below; collective vein arising from the base, less prominent than primary lateral veins, 2–4 mm from margin. *Inflorescences* erect, shorter than leaves; peduncle 28 cm long, 3 mm diam., slightly shorter than petiole, terete; spathe subcoriaceous, dark reddish purple, ovate-rounded, 8.5 cm long, 7 cm wide, broadest at or near middle, the apex round and minutely apiculate, the base cordate; stipe 1 cm long in front and back; spadix cream, cylindroid-ellipsoid, 2.1 cm long, 8 mm diam. midway, broadest at the middle; flowers rhombic, 1.5–2.4 mm long, 2–2.5 mm wide; 5–7 flowers visible in principal spiral; lateral tepals 1–1.5 mm wide, the inner margins rounded; pistils not emergent; stamens emerging well above tepals, then retracting to level of tepals, held in tight cluster above pistil; anthers 0.6 mm long, 0.6 mm wide; theca ovoid, scarcely divaricate. *Infructescence* not seen.

Anthurium hammelii is known only from the type collection made in Bocas del Toro, Panama, at 1,675 m in lower montane rainforest.

This species is distinguished by its leaves with the petiole longer than the blade, its oblong-elliptic blades, its large, ovate-rounded spathe, and cylindroid-ellipsoid, cream-colored spadix.

Anthurium hammelii is similar in overall appearance to *A. protensum* subsp. *arcuatum*, which differs in having proportionately shorter petioles, a much narrower spathe, and a more elongate, tapered spadix.

PANAMA. BOCAS DEL TORO: ENE of Cerro Pate Macho, near Finca Serrano, NE of Boquete, 1,675 m, *Hammel 6160* (MO).

Anthurium harlingianum Croat, sp. nov. TYPE: Ecuador. Napo: between Lago Agrio and Baeza at Río Oyocachi, 1,620 m, 0°20′S, 77°55′W, *Croat 50290* (holotype, MO 2819231-32; isotypes, K, NY, QCA, RSA, USM). Figures 7, 16, 149, 150, 154, 155.

Planta epiphytica; internodia brevia, 3–5(6) cm diam.; cataphyllum lanceolatum unciformie vel cucculato, persistens semi-intactum; petiolus 4.5–13 cm longus, 7–15 mm diam., adaxile uninervis, abaxile trinervis-quinquenervis; lamina (32)50–90(150) cm longa, 18–40(60) cm lata, oblongo-oblanceata; nervis primariis lateralibus 12–23 utroque. Pedunculus 21–50(100) cm longus, 3–6 mm diam.; spatha lanceolata, viridis usque ad marroninam, 6.5–22(40) cm longa, 1.5–4.5 cm lata; spadix erectus, purpureus pallescens usque ad atrasalmaneus, contractus, 10–25(47) cm longus, 4–7 mm diam. Baccae albae usque ad purpureae, oblongae, 7–8 mm longae.

Epiphytic; stem to 30 cm long; internodes short, 2.5–5(6) cm diam.; roots dense, ascending to spreading, whitish to green-gray, velutinous, to ca. 13 cm long, 3–6 mm diam.; cataphylls lanceolate and hook-shaped or cucullate, less often straight, subcoriaceous, short, to 7 cm long, persisting semi-intact. *Leaves* erect-spreading; petioles 4.5–13 cm long, 7–15 mm diam., D-shaped, obtusely angled with a medial rib adaxially, rounded to 3–5-ribbed abaxially; geniculum paler and moderately thicker than petiole, 1–2.5 cm long; sheath 2–10 cm long; blades coriaceous to subcoriaceous, broadly oblong-oblanceolate to ± elliptic, acute at apex, shallowly cordate to truncate, rarely acute to narrowly acute at base (usually in younger plants), (32)50–90(150) cm long, 18–40(60) cm wide, broadest above the middle, the margins broadly undulate; upper surface weakly glossy to matte, medium green, lower surface matte, slightly paler; midrib above obtusely raised at base, becoming acutely raised toward the apex, rounded to obtusely angled below; primary lateral veins 12–23 per side, departing midrib at 30–60° angle, ascending straight to the margin, becoming arcuate near the margin, convexly to acutely raised above, convexly raised below, slightly paler than surface above and below; tertiary veins prominulous and darker than surface below; collective vein arising from about the middle of the blade (more often absent), prominulous, 3–10 mm from margin. *Inflorescences* erect-spreading, shorter than leaves; peduncle 21–50(100) cm long, 3–6 mm diam., (2.6)4–6(11)× as long as petiole, green, sometimes tinged red-violet, terete; spathe erect-spreading to recurled, sometimes twisted, subcoriaceous to coriaceous, green to violet-purple to maroon, lanceolate, 6.5–22(40) cm long, 1.5–4.5 cm wide, inserted at 50–70° angle on peduncle, acuminate at apex, acute at base; spadix dull salmon-pink to pale violet-purple (B & K purple 5/5), rarely greenish, sessile, slightly to moderately tapered, slightly to conspicuously curved, 10–25(47) cm long, ca. 9–10 mm diam. near base, 4–9 mm diam. midway, 2–4 mm diam. near apex, broadest at the base; flowers square to rhombic or 4-lobed, 1.6–2.5 mm long, 1.5–2.4 mm wide, the sides straight to sigmoid; 6–13 flowers visible in principal spiral, (5)8–16 in alternate spiral; tepals matte to weakly glossy, minutely papillate; lateral tepals (0.4)0.8–1.3 mm wide, the outer margins 2–4-sided, the inner margins straight to slightly rounded; pistils scarcely emergent to prominently raised, gray-green to purplish; stigma oblong-ellipsoid to slitlike, 0.3–0.6 mm long, reddish to violet-purple, darker than surrounding pistil; stamens emerging from the base of spadix, in a complete sequence, the laterals preceding the alternates by ca. 13–40 spirals, the 3rd stamen preceding the 4th by ca. 2–9 spirals; anthers yellow-red (B & K yellow-red 8/2.5), 0.4–0.6 mm long, 0.3–0.9 mm wide, inclined over the pistil; thecae broadly ovoid to ovoid-triangular, slightly or not divaricate; pollen creamy white, white when dried, the scent yeasty or like rotting fruit. *Infructescence* pendent; spathe persisting; spadix 16–28 cm long, 1.5–2.5 cm diam.; berries white to violet-red, 7–8 mm long; seeds 1–2 per fruit, oblong, 1.7–3 mm long, 1.3–2 mm wide, 0.8–1.4 mm thick, with a gelatinous appendage at both ends.

Anthurium harlingianum is endemic to the lower eastern slopes of the Colombian and Ecuadorian Andes at 440 to 1,800 m (mostly above 750 m), in areas of tropical wet, premontane wet, and wetter parts of tropical moist forest, where it is almost strictly epiphytic. It occurs in a broad arc from the Serranía de Macarena in Meta Dept. in southern Colombia, to the Province of Zamora–Chinchipe in Ecuador. Probably also belonging to the same species are several Peruvian collections from the vicinity of Tingo María in Huánuco, and one each from Junín and Pasco. However, there is room for doubt, since these areas are well out of the normal range, and no collections are known from a large intervening area.

Anthurium harlingianum is distinguished by its generally large size, hook-shaped to cucullate cataphylls, erect-spreading inflorescences, and by its leaves which usually dry dark brown.

Anthurium harlingianum is closely related to

and perhaps only subspecifically distinct from *A. loretense* and *A. cataniapoense*, both of which usually occur at elevations below 300 m and occupy positions at opposite ends of the arc in the lowland Amazonian region. *Anthurium loretense* occurs at the south end of the arc in eastern Loreto Dept. in Peru, and *A. cataniapoense* occurs at the north end in the watersheds of the Río Negro and Río Orinoco in Venezuela. Both of these lowland species are distinguished from *A. harlingianum* by their pendent inflorescences and more glossy leaf blades. The blades of *A. harlingianum* are typically matte with less prominent tertiary veins than those of the other two species. Of these two species, *A. loretense* is closest to *A. harlingianum* geographically and taxonomically. It differs in having an inflorescence with both the spathe and spadix averaging about 6 cm longer than in *A. harlingianum*, and the spadix is typically more long-tapered, averaging two-thirds the length of the peduncle. In *A. harlingianum*, the inflorescence is typically erect at anthesis, but may become pendent, and the spadix is usually more stubby. It averages only about half as long as the peduncle and has a proportionally somewhat shorter spathe (ca. 3/5 as long).

All three of the above taxa share a lanceolate, usually hook-shaped cataphyll and similarly short-petiolate, coriaceous, oblanceolate leaf blades which frequently have closely set primary lateral veins at the base. In addition, all three have similarly D-shaped petiole cross sections with raised margins and an obtuse medial rib, as well as purplish violet spadices (pale purple and also ranging to other colors in the case of *A. harlingianum*).

Aside from cultivated material, the spadix of *Harling & Andersson 24496*, from Morona–Santiago, represents the lower end of spadix-length range (6.5 cm long) and is unusual in being stipitate by 5 mm. *Croat 58162*, from San Martín Dept. in Peru at 700 m, also has a stipitate spadix (6 mm in back); with its larger spadix it appears to link the last-mentioned specimen with typical material from Ecuador and with collections from further south in Peru. However, in view of its terrestrial habit on limestone rocks and leaves which dry pale green, it may represent a distinct taxon. More collections of middle-elevation *Pachyneurium* from the Department of Amazonas in Peru are needed to help solve this and similar problems in the section. Two collections from the same locality in Junín, Peru (*Killip & Smith 25528, 25604*), are unusual in being quite small for typical *A. harlingianum*, with leaf blades up to 10 cm wide, less than 50 cm long, and spadices ca. 4–7 cm long.

Anthurium harlingianum is named in honor of the Swedish botanist Gunnar Harling, who coauthored the Flora of Ecuador project with Benkt Sparre, and who has led several collecting expeditions to Ecuador.

COLOMBIA: META: Sierra de la Macarena, northern plateau, 1,000 m, *Philipson 2342* (BM, COL); Río Güejar–Río Sansa, 500–1,000 m, *Idrobo 479* (COL, US); Río Güejar–Morro Bello, El Tablazo, 500–1,200 m, *Chaparro et al. 74* (COL), *García et al. 440* (COL). PUTUMAYO: El Whiskey, S of Umbria, vic. Finca Santa Marta, *Plowman 2066* (F); Río Mocoa, 4 km E of Mocoa, 800 m, *Plowman 2027* (COL, F, GH); 700 m, 1°10′N, 76°33′W, *Croat 51762* (MO). ECUADOR: MORONA–SANTIAGO: 6 km E of Limón, rd. to La Unión, 1,300 m, *Harling & Andersson 24496* (GB); Gualaquiza, Misión Bomboiza, Misión Salesiana, 85 km NNE of Zamora, 700–800 m, 3°26′S, 78°32′W, *Sparre 19106* (S); Gualaquiza–Zamora, 5 km S of El Pangui, 800 m, 4°21′S, 78°50′W, *Croat 50816* (MO, QCA, RSA), *50817* (MO); 31 km N of Yangzatza, 1,000 m, 4°11′S, 78°49′W, *Croat 50786* (CM, MO); 20 km S of San Juan Bosco, 1,300 m, *Madison & Besse 7559* (MO, SEL). NAPO: Lago Agrio–Baeza, Río Quijos, ca. 21 km NNE of Baeza, El Chaco, 1,500 m, *Harling 3873* (S); Río Oyacachi, 23 km NNE of Baeza, N of El Chaco, 1,500–1,620 m, 0°18′S, 77°48′W, *Balslev & Madsen 10512* (AAU), *Croat 50290* (K, MO, NY, QCA, RSA, USM); 43 km E of Lago Agrio, 560 m, 0°07′N, 77°15′W, *Croat 50437* (MO); 67 km W of Lago Agrio, 760 m, *Croat 49506* (MO, QCA); 67.5 km W of Lago Agrio, 1,180 m, 0°01′N, 77°19′W, *Croat 50477* (MO, QCA); 72.5 km W of Lago Agrio, 1,166 m, *Croat 49518* (MO, NY, QCA); 74.5 km W of Lago Agrio, 1,220 m, 0°00′N, 77°20′W, *Croat 50455* (MO); Lago Agrio–Coco, 26 km N of Coco, 450 m, 0°29′S, 76°55′W, *Croat 50421* (BM, MO, US); Lago Agrio–Río San Miguel, 12.5 km N of Lago Agrio, 450 m, 0°6′N, 76°50′W, *Croat 50319* (MO, QCA); 2 km S of Río San Miguel, 21.2 km N of Lago Agrio, 470 m, 0°08′N, 76°50′W, *Croat 50350* (CM, MO, QCA, RSA), *50352* (M, MO), *50355* (AAU, CAS, CM, MO, QCA); Tena, *Asplund 10182* (S); Tena–Puyo, 1.7 km S of Río Napo, 440 m, 1°04′S, 77°47′W, *Croat 58899* (MO); Tena–Puyo, 5.5 km S of bridge over Río Napo, 510 m, 1°05′S, 77°47′W, *Croat 58922* (MO, QCA, UC); Tena–Puyo, 58–61.5 km N of Puyo, 500–600 m, *Croat 49629* (MO, QCA), *49663* (MO); Río Aguarico, road to Cepe Ferry Crossing, E of Lago Agrio, 450 m, 0°2′N, 76°50′W, *Croat 50429* (MO); Río Tena, 2 km W of Muyuna, 5.7 km W of Tena, 500 m, 0°01′S, 77°51′W, *Croat 58854* (CM, MO, QCZ); Cantón Archidona, Challuayacu, Carretera Hollin–Loreto, Km 25–31, 1,230 m, 0°43′S, 77°40′W, *Hurtado 1161* (MO); Carretera Hollin–Loreto–Coca, between Río Pucuno and Río Guamani, 0°46′S, 77°26′W, 1,100–1,200 m, *Céron 2901* (MO, QCNE); Cantón Loreto, Huaticocha, Carretera Hollin–Loreto, 575 m, *Hurtado et al. 1380* (MO); Reserva Biologica Jatún Sacha, Río Napo, 8 km E of Misahuallí, 1°4′S, 77°36′W, 450 m, *Cerón 1227* (MO, QCNE), *Palacios 2465* (MO). PASTAZA: Mera, 1,160 m, *Harling 3689, 3815* (S); Río Pastaza, Mera, *Lugo 1116* (GB); Mera–Baños, 1 km E of Topo, 1,300 m,

1°27′S, 78°10′W, *Palacios et al. 190* (MO, NY, QAME, QCNE); 3 km from turnoff from Puyo–Mera road, Tarabita, 1,000 m, *Croat 49688* (MO, QCA); Puyo–Baños, 5.7 km W of Shell, 1,070 m, 1°26′S, 78°09′W, *Croat 59076* (CM, MO, QCA); Puyo–Baños, 0.6 km E of Río Negro, 2 km W of El Topo, 1,160 m, 1°24′S, 78°12′W, *Croat 59110* (F, MO, QCA); Puyo–Macas, 19 km S of Puyo, 1,200 m, 1°37′S, 77°53′W, *Croat 50558* (MO, QCA), *50565* (MO, QCA), *50574* (CM, MO, QCA), *50576* (MO); Puyo–Macas, 33 km S of Puyo, 16 km S of Escuela Fiscal Cotopaxi, 900 m, 1°38′S, 77°52′W, *Croat 58967* (MO, QCA); 3.8 km from Puyo–Macas road, road to Canelos, 850 m, 1°37′S, 77°51′W, *Croat 58984* (MO, QCA). ZAMORA–CHINCHIPE: 2 km N of Zamora, 930 m, *Madison 2460* (SEL); carretera de PETRO–CANADA under construction, via Auca, 115 km S of Coca, S of Río Tiguino, 320 km, 1°15′S, 76°55′W, *Zak & Rubio 4318A* (MO); Loja–Zamora, 15 km above Zamora, 1,800 m, *Madison 2503* (SEL). PERU: HUÁNUCO: Tingo María Region, Prov. Huánuco, Huánuco–Pucallpa, Tingo María, Naranjillo, 600–700 m, *Ferreyra 2210* (USM, NY); Prov. Leoncio Prado, Río Huállaga, 650–800 m, *Croat 57955* (F, MO, RSA, USM), *Gentry et al. 15925* (MO), *15970* (F, MO), *Plowman & Ramírez 7568* (F, MO, US), *Solomon 3387* (MO); 25 km N of Tingo María, 1,000 m, *Winter s.n.* (*USDA PI#390586*), cult. at Univ. of Hawaii (*Kamemoto* 398) (MO); Prov. Leoncio Prado, Dtto. Rupa Rupa, Cerro Quemado, E of Tingo María, 800–850 m, *Schunke 10498* (MO); Tingo María–Pucalpa, La Divisora, 1,650 m, 9°07′S, 75°48′W, *Plowman s.n.* (Selby Garden 78-1918) (MO). JUNÍN: Pichis trail, Yapas, 1,350–1,600 m, *Killip & Smith 25528, 25601* (NY, US), *25604* (US). PASCO: Prov. Oxapampa, 20 km from Pte. Paucartambo, rd. to Oxapampa, 1,100 m, 10°41′S, 75°24′W, *Smith 7570* (MO). SAN MARTÍN: Moyobamba–Chachapoyas, 13.5 km W of Naranjos, km marker 415, 700 m, 5°38′S, 77°25′W, *Croat 58162* (MO, USM).

Anthurium holmnielsenii Croat, sp. nov. TYPE: Ecuador. Pichincha: between Pacto and Nuevo Azuay, 15.3 km N of Pacto, 1,320 m, 0°11′N, 78°04′W, *Croat 61640* (holotype, MO 3422019; isotypes, B, K). Figures 156, 157, 159–161.

Planta epiphytica vel terrestris; internodia brevia, 1.5–3.5 cm diam.; cataphyllum lanceolatum, persistens fibris linearis; petiolus (18)24–47 cm longus, 7–12 mm diam., acute D-formatus; lamina coriacea, oblongo-oblanceolata aut oblanceolata-elliptica, apice longo-acuto, basi anguste acute, (50)76–98.5 cm longa, (11)13–27 cm lata; nervo collectivo e basi. Pedunculus 24–64 cm longus, 3–6 mm diam., 1.4–2-plo longiorus quam petiolo; spatha 6–17.5 cm longa, 1.5–2.7 cm lata; spadix 9–20.5 cm longus, viridis, longe contractus; baccae aurantiacae, 3.5–4.7 mm longae, 2.3–2.7 mm latae.

Epiphytic, occasionally terrestrial; stem 1.5–3.5 cm diam.; leaf scars 1.5–1.7 cm high, 2.2–2.5 cm wide; roots dense, descending, pale, moderately elongate; cataphylls coriaceous, lanceolate, 17–25 cm long, narrowly acute at apex, drying light brown to tan, persisting as linear fibers at the apex of the stem. *Leaves* spreading; petioles (18)24–47 cm long, 7–12 mm diam., sharply D-shaped and slightly thicker than broad, broadly convex to weakly ribbed medially adaxially, the margins sharply raised to winged, rounded abaxially; geniculum thicker and paler than petiole, becoming fissured transversely with age, 1–3 cm long; blades coriaceous, oblong-oblanceolate to oblanceolate-elliptic, long-acuminate at apex, narrowly acute at base, (50)76–98.5 cm long, (11)13–27 cm wide, the margins broadly undulate; upper surface matte to semiglossy, dark green, lower surface semiglossy to glossy, slightly paler; both surfaces drying concolorous, green to yellowish; midrib above prominently convex and paler than surface, below thicker than broad at base of the blade, becoming prominently convex toward the apex and paler than surface; primary lateral veins numerous, to more than 20 per side, departing midrib at 45–60° angle, ± straight to the collective vein, moderately obscure, weakly sunken to raised above, darker than surface and weakly raised below; interprimary veins almost as conspicuous as primary lateral veins, numerous; tertiary veins obscure, raised on drying; collective vein arising from near the base, weakly sunken above, equally as prominent as primary lateral veins on drying and when fresh, 5–25 mm from margin. *Inflorescences* spreading; 24–64 cm long, 3–6 mm diam., 1.4–2(3.4)× as long as petiole, green tinged with purple, terete; spathe erect to spreading, subcoriaceous, green, sometimes heavily tinged purplish or red, broadly lanceolate to oblong-lanceolate, 6–17.5 cm long, 1.5–2.7 cm wide, broadest near the base, acuminate at apex (the acumen inrolled), acute to obtuse at base; stipe 1–2.2 cm long in front, 1–2 mm long in back; spadix green (B & K yellow-green 5/5), also reported as brownish, long-tapered, subsessile, straight to prominently curved, 9–20.5 cm long, 6–9 mm diam. near base, 3–4 mm diam. near apex; flowers square, 2.3–2.7 mm in both directions, the sides smoothly to jaggedly sigmoid; 7–8 flowers visible in principal spiral, 4–5 in alternate spiral; tepals matte, densely and minutely papillate; lateral tepals 1.2–1.4 mm wide, the inner margins straight, the outer margins 2–4-sided; pistils slightly raised, minutely papillate, green; stigma linear, 0.4–0.5 mm long, the laterals preceding the alternates by 8–9 spirals, the 3rd stamen preceding the 4th by 1–3 spirals; filaments fleshy, translucent, somewhat flattened, 0.7–0.8 mm wide; anthers dark yellow, 0.6–0.8 mm long, 0.6–0.9 mm wide; thecae oblong-ovoid, not divaricate; pollen orange. *Infructescence* with the spathe persisting; spadix 16.8–31 cm long,

1.4–2.3 cm diam.; berries orange, oblong-ovoid, slightly beaked, 6.5–7.4 mm long, 4–4.5 mm diam.; pericarp somewhat thickened, with linear raphide cells; mesocarp transparent, gelatinous; seeds 1–2 per berry, yellowish brown when dried, oblong, sometimes ovoid, 3.5–4.7 mm long, 2.3–2.7 mm diam., 1.6–2 mm thick, with a gelatinous, sticky appendage at both ends.

A member of series *Multinervia*, *Anthurium holmnielsenii* is known only from Ecuador in the provinces of Los Ríos, Imbabura, Pichincha, and Cotopaxi at 250 to 1,500 m in tropical moist and premontane wet forest, where it grows either terrestrially or as an epiphyte.

This species is distinguished by its concolorous, green-drying leaf blades with numerous primary lateral veins and a collective vein arising from near the base, sharply D-shaped petioles, long-tapered, green spadix, and orange berries.

Anthurium holmnielsenii is closely allied to *A. acutissimum*, and differs in having petioles with sharply raised margins and spreading-pendent to more or less erect leaves with broader blades (3.3–6.5(7) vs. (6.7)7.5–10(11) times longer than broad).

This species is named in honor of Lauritz B. Holm-Nielsen, who has coordinated much of the botanical activity in Ecuador by the University of Aarhus, Denmark.

ECUADOR. COTOPAXI: Río Guapara, 20 km NW of El Corazón, 250 m, *Sparre 17113 bis* (S). IMBABURA: Colloapi, 840 m, *Solís 12889* (F). LOS RÍOS: Río Blanco, Santo Domingo–Esmeraldas, 3 km S of Km 24, 250 m, 0°5′S, 79°15′W, *Croat 50689* (K, MO, QCA). PICHINCHA: El Paraiso–Saguangual, 3 km from El Paraiso, 1,500 m, 0°10′N, 78°46′W, *Oellgaard et al. 37773* (AAU); Pacto–Nuevo Azuay, 5 km N of La Esperanza, 1,300 m, *Holm-Nielsen et al. 24542* (AAU, MO); 15.3 km N of Pacto, road, 2.3 km N of Paraiso, 1,320 m, 0°11′N, 78°04′W, *Croat 61640* (B, K, MO).

Anthurium iramirezae Bunting, Ann. Missouri Bot. Gard. 76: 917–918, 1989. TYPE: Venezuela. Amazonas: Dpt. Río Negro, Serranía de Tapirapeco, outcrop of granitic rocks, 1,350 m, 1°20′N, 64°55′W, *I. Ramirez & Laskowsky 310* (holotype, VEN). Figure 353.

Epilithic; stem thick, reclining horizontally; internodes short; cataphylls persisting. *Leaves* few; petioles 19–40 cm long, subterete, sulcate adaxially, the margins rounded; geniculum 1.7–2.3 cm long, 1–1.2 cm thick; blades held erect on petioles, ovate, obtuse to short-acuminate at apex (the acumen with a cusp to 1.3 cm long), cordate at base, 30–37 cm long (equaling or twice as long as petioles), 19–24 cm wide (1.5–1.7× longer than wide); sinus arcuate; upper surface glossy, lower surface slightly paler and brown glandular-punctate; major veins prominently raised on upper surface; basal veins 2 pairs, free to base (not naked at the sinus); primary lateral veins 7(8) per side, departing midrib at 45–55° angle, almost straight or weakly arcuate-ascending to the margin; tertiary veins prominent on both surfaces. *Inflorescences* longer than leaves; peduncle 45–71 cm long; spathe recurved or reflexed, persistent, green, narrowly oblong-ovate, 11 cm long, 0.8 cm wide, decurrent at base for 8 mm; spadix dark purple, becoming green with age, slightly tapered, sessile, 13.3–15.3 cm long, 7.5 mm diam.; 6–8 flowers visible in principal spiral. *Infructescence* to 1.5 cm diam.; berries unknown.

Anthurium iramirezae is endemic to Venezuela, known only from the type locality in an area of premontane rainforest, at 1,250 m.

The description given here is based only on the original type description and the species is therefore imperfectly known.

This species is distinguished by its broadly ovate, subcordate, glandular-punctate blades and narrowly oblong-ovate spathe.

It is most closely related to *A. guanchezii*, but that species differs in having the geniculum remote from the base of the leafy portion of the blade, as well as by having naked basal veins and a narrowly ovate spathe which is 3.6× longer than broad.

Anthurium iramirezae is perhaps most easily confused with *A. wurdackii*, but that species has proportionally narrower (about 1.9× longer than broad) blades with angular rather than acute sinus and epunctate lower surface, and its spathe decurrent for 3.5 to 7.5 cm.

VENEZUELA. AMAZONAS: Río Negro, Serranía de Tapirapeco, outcrops of granitic rocks, 1,350 m, 1°20′N, 64°55′W, *Ramirez & Laskowsky 310, 318* (VEN).

Anthurium jenmanii Engl., Pflanzenr. IV. 23B(Heft 21): 72. 1905. TYPE: Guyana. Esequibo, *Jenman 5760* (lectotype, K; isolectotypes, BRG, NY).

Anthurium englerianum Bunting, Acta Bot. Venez. 10: 270. 1975. TYPE: Venezuela. Monagas: between Guáchardo & Cueva del Guácharo, 1 km above El Guácharo, *Bunting 2653* (holotype, MY).

Anthurium trinitatis Engl., Pflanzenr. IV. 23B(Heft 21): 73. 1905. TYPE: Trinidad, *Fendler 741* (holotype, K; isotype, NY).

Epiphytic, epilithic or terrestrial; stem short, (1)1.5–3 cm diam.; roots dense, spreading to ascending, pale green to brownish, thick and blunt, ca. 5–10 cm long, 3–6 mm diam.; cataphylls

broadly lanceolate, subcoriaceous to coriaceous, (3)5–7 cm long, acute at apex, drying dark brown, persisting semi-intact or as a reticulum of fibers. *Leaves* erect to erect-spreading; petioles (3)7–20(38) cm long, 6–15 mm diam., bluntly to sharply D-shaped, flattened to weakly convex adaxially, rounded abaxially, the surface pale-speckled; geniculum slightly paler and moderately thicker than petiole, 0.5–2.5 cm long; sheath 1–6 cm long; blades coriaceous, broadly oblanceolate to elliptic (rarely ovate-elliptic), shortly and abruptly acute (rarely long-acuminate or obtuse-rounded) at apex, narrowly acute to obtuse to broadly truncate to sometimes weakly subcordate at base, (22)40–103 cm long, (8)11–52 cm wide, broadest near the middle or in the upper fourth, the margins moderately and broadly undulate; upper surface semiglossy to glossy, yellowish green, lower surface matte to weakly glossy, moderately paler, drying yellow-green, matte; midrib flat at base, soon becoming bluntly acute above and conspicuously paler than surface, prominently convex to higher than broad at base, becoming obtuse-rounded toward the apex below, slightly paler than surface; primary lateral veins 5–13 per side, departing midrib at 30–60° angle, broadly arcuate-ascending to the margin, the uppermost merging into a collective vein, raised near midrib, sunken at margin, moderately paler than surface above and below; interprimary veins absent except near the base, less conspicuous than primary lateral veins; tertiary veins sunken above, raised below, raised when dried; reticulate veins prominulous above and below when dried; collective vein arising in the upper third of blade or absent, equally as prominent as primary lateral veins, 6–15 mm from margin. *Inflorescences* spreading-erect to spreading-pendent, equaling or longer than leaves; peduncle 26–86 cm long, 5–9(15) mm diam., 3.4–6× as long as petiole, pale-speckled, colored like petiole, sometimes ringed with purple, terete to elliptic; spathe reflexed, usually soon withering and becoming twisted, subcoriaceous, pale green tinged with purple, becoming purple at anthesis, oblong to lanceolate, 11–50 cm long, 1.5–4.5 cm wide, broadest near the base, inserted at 30–60° angle on peduncle, acuminate at apex (the acumen 8 mm long), narrowly acute to obtuse, sometimes decurrent for 3–4 cm at base; stipe absent or to 4–5 cm long in front, to 1 cm long in back; spadix dark maroon to dark purple, sometimes bluish pre-anthesis, tapered to cylindroid, usually sessile to weakly stipitate, nearly straight to slightly curved, 10.4–47 cm long, 6–9(12) mm diam. near base, ca. 4 mm diam. near apex, broadest at the base; flowers rhombic, 1.8–2.7 mm long, (1.3)1.7–2.2 mm wide, the sides straight to slightly sigmoid; 6–14 flowers visible in principal spiral, 6–10 in alternate spiral; tepals matte to semiglossy, minutely papillate; lateral tepals 1–1.2 mm wide, slightly convex, erose, the outer margins 2-sided; pistils not emergent, whitish; stigma slitlike, colored like tepals, 0.5 mm long; stamens emerging in a slow, regular sequence from the base, the laterals preceding the alternates by 7–12 spirals, the 3rd stamen preceding the 4th by 1–8 spirals, held against the pistil and obscuring it; anthers pale yellow to orange, 0.4–0.5 mm long, 0.5–0.7 mm wide; thecae ovoid, divaricate; pollen yellow, fading to whitish, moderately sweet-scented. *Infructescence* pendent; berries pale reddish purple to purple or white tinged with violet apically, obovoid, rounded at apex, to 10 mm long, 7 mm diam.; seeds 2 per berry, oblong to obovoid, 8 mm long, 3 mm diam.

Anthurium jenmanii ranges from Trinidad and Tobago and Venezuela (Sucre and Monagas; one collection from northeastern Bolívar) to Guyana, Surinam, French Guiana, and Amapá in Brazil. It is the only species, besides *A. fendleri*, which is extra-Amazonian in northern South America and which also occurs in lowland Amazonia. Instead of achieving this via the Guianas, *A. fendleri* ranges south to the departments of southern Colombia. *Anthurium jenmanii* occurs mostly below 500 m in moist forest as well as in dry open woodlands and granite outcrops, where it may be terrestrial, epiphytic, or epilithic.

This species is recognized by its large, coriaceous blades with impressed tertiary veins on the upper surface (when fresh), which usually dry yellow-green. Also characteristic are its purple spadix and spathe, the latter usually withering early, and by its reddish purple berries. The leaf bases are highly variable, ranging from acute to somewhat subcordate (see below). Staminal progression is markedly slow, the spadix requiring over one month under office conditions (room temperature) to complete anthesis throughout its length of 14 cm.

Specimens from throughout the range of *A. jenmanii* may have basally obtuse-rounded or even subcordate leaf blades; *Sheffer 265*, originally collected in Trinidad and cultivated at the University of Hawaii, and *Sastre 1665*, from the Tumuc-Humac Mountains in Brazil, are examples of the latter end of the spectrum. One collection, *Geyskes 16*, from the Tumuc-Humac Mountains along the Brazilian border in Surinam, is noteworthy in having leaf blades conspicuously pustular on the lower surface. This character is typical for *Anthurium*

bonplandii subsp. *guayanum*, but that subspecies typically has often dark, plate-shaped glands in addition and occurs at higher elevations; no collections of the latter are known from the Tumuc-Humac Mountains. *Sastre 1665* and *Granville 1179*, also from these mountains, are more typical of *A. jenmanii* and have no pustules on the leaf blades. This region is in general poorly known, and further collections would greatly help to understand the geographical distribution and variation of *A. bonplandii* and *A. jenmanii*, and also *A. cataniapoense*. Another noteworthy collection is *Cremers 7405*, from north-central French Guiana, which is aberrant in having a leaf blade so attenuate at the base that the geniculum appears remote from the blade by up to 4.5 cm.

In 1975, Bunting described *A. englerianum*, based on material collected in Sucre in the Coastal Cordillera of Venezuela, 1 km above Guácharo. Examination of the type and material collected at the same site (*Croat 54389*) revealed no characters that can be used to separate *A. englerianum* from *A. jenmanii*, despite the fact that the type locality of *A. englerianum* is at 970 m elevation. It is here synonymized for the first time.

WITHOUT LOCALITY. *Potter 5299* (NY); cultivated, *Croat 45053* (MO). BAHAMAS. Cultivated, Nassau, New Providencia, *Moore 7023* (BH). BRAZIL: Serra Tumucumaque, Massif du Mitaraka, 500 m, *Sastre 1665* (CAY, US). AMAPÁ: Roche, Cachoeira Grande, *Irwin et al. 47417* (IAN, NY); Cachoeira Utussansain, island in Cachoeira, *Irwin et al. 48000* (NY, US); Rio Araguari, downriver from Pôrto Platon, *Pires et al. 51152* (NY); Rio Jari, Cochoeiras das Aurucuopatari, 120 m, 0°28′N, 53°7′W, *Egler & Irwin 46468* (NY, US, MG); Rio Maraca, Mazagão, *Rabelo et al. 2200, 2210* (NY); Rio Oipoque, near Mt. Carupina, 10–80 m, 3°33′N, 51°37′W, *Pires & Westra 48823* (US); Cachoeira Grande Roche, *Froes 26695* (IAN, RB), *Luetzelburg 20265* (M); AMAPÁ–PARÁ: Serra Tumucumaque, via Rio Cumina, *Sampaio 5267, 5424* (RB). FRENCH GUIANA. WITHOUT LOCALITY: *Hay 2827*: cultivated at M (*#84/3632*) (MO); W Bas Oyapock, Haut de la Cirque Armontabo, *Cremers 7047* (CAY, K); Bassin du Ha, Akouba Booka goo Soula, 160 m, *Granville et al. 9779* (CAY, P, US); Bassin du Haut-Marouini, 230 m, *Granville et al. 9908* (CAY), 200 m, *9291* (CAY); Bassin de l'Oyapock, 10 m, *Cremers 9936* (CAY); Camopi River above its mouth at Tamouri River, *Granville 2097* (CAY, US); Grand Canori, *Oldeman 1979* (CAY); Montagne Maripa, *Granville 2870* (CAY, P); Pedra Alice, *Irwin et al. 47566* (NY); opposite Pedra Alice, *Irwin et al. 47604* (NY); Savanes-Roches, Fleuve Oyapock, *Oldeman 2575* (MO); St. Elie, *Prevost 740* (CAY); NW of Sinnamary, W of Orstom "Ecrex" Project, St. Elie Track, 250 m, *Croat 53848* (MO); Brazilian border, Trois Sauts, 300–350 m, *Grenand 1091* (CAY, P); Massif des Emerillons, 450 m, *Cremers 6594* (CAY, K); 300–350 m, *Cremers 6639* (CAY); Montagne des Trois Pitons, second peak, *Oldeman 2609* (CAY, US); Monts de la Trinite, Inselberg NW of Monts de la Trinité, *Cremers 7405* (K); Mt. St. Marcel, Haut Oyapock, 300–450 m, *Sastre 4412* (P); Haut Tampoc, S of Pier Kourou, *Cremers 4517* (CAY); Tumuc-Humuc, *Granville 1179* (CAY, P); Brazil and Surinam border, summit of Paloulouimeenpeu, 707 m, *Granville 1103* (CAY, K, MO). GUYANA: Cayenne, *Fevillet 1126* (U); Tumatumari, *Gleason 172* (NY); Rockstone, *Gleason 617* (GH, NY); Mazaruni station, *Forestry Dept. 2939* (K); Quebrada Camonnie, *Jenman 2026* (K); Demerara River, Christianburg, *Bartlett s.n.* (BRG); Río Essequibo, Morabilli Creek, near Bartica, 0 m, *Sandwith 427* (K); Mazaruni River, upper part, *Leng 355* (NY); Potaro–Siparumi Region. Chenapou, Amerindian village (Patumona), 50 km upstream from Kaieteur Falls, 450 m, 5°00′N, 59°34′W, *Kvist et al. 302* (US). ESSEQUIBO: *Jenman 5760* (BRG, K, NY); Bo River, Kurihi Falls, *Forestry Dept. 7060* (K, NY). HAWAII. Cultivated at Pacific Tropical Bot. Gard. *Croat 44872* (MO, SEL). SURINAM: Cultivated, originally collected by Dodson, Paramaribo, *Madison 1927* (SEL); Nassau Mts., Marowijne River, 550 m, *Cowan & Lindeman 39100* (F, NY, US, U); Paloemeu River, Palaimee Savannah, *Geyskes s.n.* (U); Tumuc–Humac Mts., Temomairem, 200 m, 3°00′N, 55°23′W, *Geyskes 16* (U, NY); Wosuna Falls, 300 m, *Daniels & Jonker 833* (NY, U). SARAMACCA: Wilhelmina Gebergte, WSW of Juli Anatrop, *Werkhoven 16712* (BBS, SEL). TOBAGO. Great Dog River, *Eggers 5802* (US); Little Tobago, *Broadway 4909* (US), *Dinsmoore 38* (WIS), *Purseglove 6325* (K, US); Mason Hall, *Broadway 4832* (US). TRINIDAD: *Broadway 4106* (BM), *Fendler s.n.* (BM), *Fendler 741* (BM), *Hart s.n.* (TRIN); Cultivated, *Bailey & Bailey s.n.* (BH); Tabaquite, Monserrat Hills, *Jermy 2543* (cult. at Kew) (K); Arima–Blanchisseuse, milepost 18.75, 30–60 m, *Simmonds 126* (K); Caspar Grande, Pt. Baleine, 30 m, *Simmonds 82, 116* (K, TRIN); Cumaca road, turnoff 2 mi. E of Valencia, 200 m, *Croat 53918* (MO); Hart's Cut to Belle View, *Britton & Bailey 2236* (K, NY); Matura–Valencia, Mi. 8, E of Valencia, less than 150 m, *Croat 53915* (MO); Moruga, *Broadway 7621* (TRIN); Pointe Gourde, overlooking Telephone Bay, *Philcox 8084* (K, NY); Port of Spain, *Broadway 4176* (K), *Elmore R9* (LAM); Rapsey, *Sheffer 265* (MO); Teteron Bay, *Broadway 6886* (BM, MO); Valencia, *Britton & Britton 2101* (K, NY); Gasparee Island, *Britton & Coker 554* (NY, US); Guaico–Manzanilla Reserve 30–60 m, *Philcox et al. 8034* (K); Matura Forest Reserve, Toco Road, 50 m, *Philcox et al. 8075* (K); Monos Island, *Williams s.n.* (TRIN); en route to Huevos Island, Gulf of Paria, *Ewan 17050* (BM, GH). VENEZUELA. BOLÍVAR: Altiplanicie de Nuria, E of Miamo, 500–600 m, *Steyermark 88526* (NY, US); Río Toro (Río Grande) Río La Reforma–Puerto Rico, N of El Palmar, 200–250 m, *Steyermark 88110* (F, NY, US, VEN). MONAGAS: El Guácharo–La Cueva del Guácharo, *Bunting 2653* (MY, NY), *4351* (NY); 1.5 km above Guácharo, 1.5 km below Cuevas del Guácharo, 970 m, 10°10′N, 63°31′W, *Croat 54389* (B, MO, VEN). SUCRE: El Pilar–Guariguen, 4–10 km S of El Pilar, 10°31′N, 63°06′W, *Croat 54382* (F, IBE, K, M, MO, SEL, US); Quebrada del Purgatorio, E of Grapa, *Lasser & Vareschi 3851* (VEN); Península de Paria, Cerro Patao, 300 m, 10°41′N, 62°3′W, *Milliken et al. 38* (MO); Cristóbal Colón, *Broadway 170* (GH, NY, US); Cumanacoa–Caripe, La Cuestra, 6 km NW of Las Piedras, 760 m, *Bunting 2697, 2697S* (NY); Lago de Guanoco, *Lasser & Vareschi 3906* (VEN); Dtto. Cajigal, Santa Isabel, *Fernandez 3349* (MY).

Anthurium johnsoniae Croat, sp. nov. TYPE: Originally collected in Colombia. Magdalena: between Santa María and El Campano, vic. of Minca, road above Santa María via Bonda, cultivated by Marilyn and Al Johnson, *Croat 62835* (holotype, MO 3656446).

Planta terrestris; internodiis brevibus, caule 1–3 cm diam.; cataphyllum persistens intactum mox deciduum; petiolus D-formatus vel quadrangularis, complanatus adaxialiter, 2–3 costatus abaxialiter; lamina late oblanceolata, (24)50–70 cm longa, (11)17–30 cm lata; nervis primariis lateralibus 6–16 utroque, sub angulo circa 50°–90°; pedunculus 24 cm longus; spatha lanceolata, viridis, 9.8 cm longa, 1.4 cm lata; spadix longe protractus, purpureus in apice, ochraceus ad basim. Baccae ignotae.

Stem short, ± slender, 15–50 cm long, 1–3 cm diam.; roots moderately numerous, spreading to descending, grayish white to whitish green, glabrous, minutely but conspicuously warty, elongate, weakly tapered, 3–5 mm diam.; cataphylls thinly subcoriaceous, narrowly straight-lanceolate, prominently 1-ribbed throughout, 7–18 cm long, acute to obtuse and with subapical apiculum, pale green (B & K yellow-green 6/5), drying reddish brown (B & K yellow-red 4/7.5), persisting intact, eventually deciduous. *Leaves* erect to spreading; petioles 12–29 cm long, 4–10 mm diam.; D-shaped to quadrangular, flattened to shallowly sulcate adaxially, sometimes with the margins weakly raised, prominently 2–3-ribed abaxially; geniculum thicker than petiole, becoming fissured transversely with age, 1.3–2 cm long; blades subcoriaceous, broadly oblanceolate, abruptly and shortly acuminate at apex (the acumen apiculate), obtuse to acute to narrowly acute at base, (24)50–70 cm long, (11)17–30 cm wide, broadest above middle, the margins broadly undulate; upper surface weakly glossy, dark to medium green (B & K yellow-green 3/10), lower surface semiglossy to weakly glossy, moderately paler; midrib flat at base, becoming obtusely and narrowly angular toward the apex above, paler than surface, prominently higher than broad with sharp ridge at base, becoming convexly raised and flat toward the apex below; primary lateral veins 6–16 per side, departing midrib at 50–90° angle, straight to weakly arcuate, convexly raised, much paler than surface above, slightly raised below; tertiary veins obscure above and darker than surface below; collective vein arising from below the middle, weakly sunken above, slightly darker than surface below, 3–7 mm from margin. *Inflorescences* with peduncle 24 cm long, 3–5 mm diam., 0.9× as long as petioles, green subterete; spathe reflexed, subcoriaceous, green, lanceolate, 9.8 cm long, 1.4 cm wide, broadest near the base, acute at apex (the acumen inrolled, 3 mm long), acute and somewhat decurrent at base; spadix maroon in the upper ⅓, brownish yellow-ochre at base (B & K yellow 5/5), long-tapered, sessile to subsessile (stipe to 2 mm long), slightly curved, held at 160° angle from peduncle, (7)16–22 cm long, 5–8 mm diam. near base, 2–3 mm diam. near apex, broadest at the base; flowers rhombic to square, 1.5–2 mm long, 1.2–1.5 mm wide, the sides straight, becoming smoothly sigmoid; 7–8 flowers visible in principal spiral, 10–12 in alternate spiral; tepals densely and minutely papillate; lateral tepals 0.8–1 mm wide, the inner margins broadly rounded, the outer margins 2–3-sided; pistils not seen; stamens barely emerging above level of tepals and persisting, the laterals preceding the alternates by 12–14 spirals, the 3rd stamen preceding the 4th by 7–8 spirals, held in a tight cluster above the pistil; anthers yellow, 0.4–0.5 mm long, 0.5 mm wide, obscuring pistil; thecae oblong-ovoid, slightly divaricate; pollen bright yellow. *Infructescence* with the spathe persisting; spadix 23 cm long, 2.8 cm diam., bearing berries in the basal portion only; berries orange, broadly ellipsoid, apparently truncate and with radial ridges at apex, 10–12 mm long, 4.8–5 mm diam.; seeds 2 per berry, dark yellowish with numerous pale raphides on the surface, oblong, flattened, 4.7–6 mm long, 2–2.5 mm diam., 1.2–1.7 mm thick.

Anthurium johnsoniae is known only from a live collection made by Marilyn and Al Johnson near Minca in Magdalena Province in Colombia, apparently in a premontane wet forest life zone.

This species is distinguished by its glabrous, minutely warty roots, leaf blades with primary lateral veins spreading at a broad angle and with a collective vein mostly arising from near the base, and by its ellipsoid, orange berries.

Because of the broadly spreading primary lateral veins and basal collective vein origin, *A. johnsoniae* resembles most closely *A. caucavallense*, also from Colombia, which has smooth roots and purple berries.

The species is named in honor of one of the collectors, Marilyn Johnson, of Miami, Florida.

COLOMBIA. MAGDALENA: between Santa Marta and El Campano, vic. of Minca, road above Santa María, via Bonda, originally collected by Marilyn & Al Johnson, *Croat 62835* (B, COL, K, MO, NY, US).

Anthurium knappiae Croat, sp. nov. TYPE: Peru. San Martín: Lumas, on old trail from Yumbatos to San Antonio de Cumbasa, S of Shapajilla, lower slopes of Cerro Isco, 400–500

m, *Knapp et al. 8544* (holotype, MO 3483655; isotypes, B, US, USM).

Planta epiphytica; caulis ignotis; cataphyllum persistens in fibris pallidus; petiolus 34.5–42 cm longus, 6–7 mm diam., sulcatus; lamina late elliptica, 57–61 cm longa, 18–19.5 cm lata, basi attenuata; pedunculus 74–93 cm longus, 4–5 mm diam.; spatha lanceolata, viridis, 10–12 cm longa, 1–1.3 cm lata; spadix cremeus vel viridis, cylindroidius, 6–11 cm longus, ca. 4 mm diam.

Description based on dried material only. Epiphytic on rotten logs; stem unknown; cataphylls ca. 7 cm long, apparently persisting as weathered pale fibers. *Leaves* erect-spreading; petioles 34.5–42 cm long, 6–7 mm diam., sulcate with the margins apparently acute, apparently acutely 1-ribbed abaxially; geniculum ca. 1 cm long; sheath 4.5 cm long; blades subcoriaceous, broadly elliptic, acuminate at apex, long-attenuate at base, 57–61 cm long, 18–19.5 cm wide, broadest at or near the middle, the margins flat, both surfaces yellow to olive-green; midrib convexly raised above, prominently raised and apparently acutely angled toward the base below; primary lateral veins 12–16 per side, departing midrib at 50–80° angle, slightly arcuate to the collective vein, weakly raised above and below; interprimary veins much less to almost as conspicuous as primary lateral veins; reticulate veins weakly raised; collective vein arising from the base, equally as prominent as primary lateral veins, 10–16 mm from margin. *Inflorescences* erect; peduncle 74–93 cm long, 4–5 mm diam., 1.8–2.4× as long as petiole, green, terete; spathe spreading to reflexed, subcoriaceous, green, lanceolate, 10–12 cm long, 1–1.3 cm wide, broadest near the base, inserted at ca. 20° angle on peduncle, acuminate at apex (the acumen with apiculum 4 mm long, inrolled and recurled), prominently decurrent for 2–3 cm at base; spadix "creamy," probably somewhat greenish (post anthesis), cylindroid, sessile, 6–11 cm long, 4 mm diam.; flowers square, ca. 4 mm in both directions; 5–6 flowers visible in principal spiral, 4–5 in alternate spiral; tepals with conspicuous pale raphide cells; lateral tepals 1–2 mm wide, the inner margins broadly rounded, the outer margins 2-sided; anthers 0.8–1 mm long, 1.4–1.8 mm wide, inclined over the pistil; thecae ovoid, slightly divaricate. *Infructescence* (immature) erect-sreading; spathe persisting, green; spadix 8 cm long, 1 cm diam.; berries green, ellipsoid.

Anthurium knappiae is endemic to Peru, known only from the type locality, at 400 to 500 m, probably in an area of premontane wet forest. The type specimen was collected in the Tarapoto region, about 20 km north of Tarapoto. It is one of six or more *Pachyneurium* species from this region.

This species is distinguished by its broadly elliptic, long-petiolate leaves which dry green and have the collective vein arising from near the base, and by its long-pedunculate inflorescence with a greenish spadix.

This species is most closely related to *A. oxycarpum*, differing in its petiole being 2–3× longer, its attenuate leaf base (only rarely attenuate for *A. oxycarpum*), its much longer peduncle (74–93 cm long vs. 18–55 cm long for *A. oxycarpum*), and its pale, raphide-cell-covered, nonglaucous tepals (vs. conspicuously glaucous and apparently free of raphide cells in *A. oxycarpum*).

The new species is named in honor of Sandra Knapp, who made the type collection.

PERU. SAN MARTÍN: Cerro Isco, lower slopes, old trail from Yumbatos to San Antonio de Cumbasa, Lumas, S of Shapajilla, 400–500 m, 6°20′S, 76°24′W, *Knapp et al. 8544* (B, MO, US, USM).

Anthurium krukovii Croat, sp. nov. TYPE: Brazil. Amazonas: Maraa, Rio Japurá, Lago Maraa, vic. of Maraa, 1°51′S, 65°36′W, *Plowman et al. 12211* (holotype, INPA; isotype, MO 3117449).

Planta terrestris aut epiphytica; internodia brevis, 5–10 mm diam.; cataphyllum lanceolatum, persistens intactum; petiolus 19.5–38 cm longus, 3–7 mm diam., subteres, anguste sulcatus; lamina ovato-elliptica, 26–40 cm longa, 11–18 cm lata; geniculum remotus 4–11 cm; pedunculus 31–57.5 cm longus, 3–4 mm diam.; spatha oblongo-lanceolata, 8 cm longa, 7 mm lata; stipes 1.5–3.5 cm longus; spadix atrorubens ad brunneus, 12–15 cm longus, 4–5 mm diam.; baccae violaceae.

Description based on dried material only. Terrestrial or epiphytic; stem 5–10 mm diam.; roots dense, numerous, spreading, pubescent, relatively short, bluntly pointed, 1–5 mm diam.; cataphylls lanceolate, thin, 4–8 cm long, acute at apex, brown, persisting intact, eventually deciduous. *Leaves* with petioles 19.5–38 cm long, ca. 3–7 mm diam., subterete, narrowly sulcate with rounded margins adaxially, rounded abaxially; geniculum darker than petiole, 0.6–1.5 cm long; blades subcoriaceous, ovate-elliptic, long-acuminate at apex, acute to semirounded at base, then narrowing abruptly to the geniculum (making geniculum seem remote from base by 4–11 cm), 26–40 cm long, 11–18 cm wide, broadest below or near the middle, the margins concave toward the base, apparently shallowly undulate; surface semiglossy, green to yellowish green; midrib narrowly convex above, sharply acute below; primary lateral veins 7–10 per side, de-

parting midrib at 40–65° angle, ± straight, raised above and below, more sharply so below; tertiary veins weakly raised; reticulate veins obscure above, weakly raised below; collective vein arising from near the base to about the middle of the blade, equally as prominent as primary lateral veins, 5–15 mm from margin. *Inflorescences* with peduncle 31–57.5 cm long, ca. 3–4 mm diam., equaling or to 1.8× longer than petiole, light to olive-green, terete; spathe recurled, membranous, pale reddish green, oblong-lanceolate, to 8 cm long, ca. 0.7 cm wide, broadest near the base, narrowly acute at apex, acute and decurrent at base; stipe 1.5–3.5 cm long in front, (0)8–17 mm long in back; spadix dark red to brown, long-tapered, usually long-stipitate, 12–15 cm long, 4–5 mm diam. near base, ca. 2 mm diam. near apex; flowers ± square or rhombic when dried, 1.2–1.8 mm in both directions, the sides straight to smoothly sigmoid; 5–7 flowers visible in principal spiral, 8–9 in alternate spiral; lateral tepals 0.9–1.2 mm wide, the inner margins straight to broadly rounded, the outer margins 2-sided; pistils emergent, not raised; stigma ellipsoid, 0.5–0.7 mm long; anthers 0.2–0.3 mm long, 0.4–0.5 mm wide, inclined over pistil; thecae ovoid, slightly divaricate. *Infructescence* with spathe deciduous; spadix ca. 1 cm diam.; berries violet, (rehydrated) globose to oblong-ovoid, rounded at apex, 3.5–3.7 mm long, 2.6–3.5 mm diam.; pericarp somewhat thickened with moderately numerous pale raphide cells; seeds 1 or 2 per berry, brown, oblong-ovoid, somewhat flattened laterally, 2.5–2.8 mm long, 1.8–2 mm diam., 1.2–1.4 mm thick.

Anthurium krukovii is known from a few collections made in the central, northern and southwestern parts of Amazonas, Brazil, below 150 m, probably in a tropical moist forest life zone.

The species is characterized mainly by the shape of its leaf blades, which are rounded and abruptly attenuate at the base and narrowed even further to the geniculum in a manner that makes the latter seem remote from the base of the blade by 4–11 cm.

Anthurium krukovii is mostly closely allied to *A. atropurpureum* var. *arenicola*, which differs in having more coriaceous and usually narrower leaf blades which are long-attenuate (with more or less parallel margins) toward the base, and in having mostly shorter petioles. The same general differences apply to the typical variety of *A. atropurpurem*, which is smaller in overall size.

The occurrence of clear pustules on the undersurface of the dried leaf blades in the present species is of interest. The same feature occurs, albeit rarely, in *A. atropurpureum*, the presumed closest relative of *A. krukovii*. The two collections of *A. krukovii* which show this feature are *Byron et al. 621* and *Duarte 6958*.

The new name *Anthurium krukovii* honors Boris Alexander Krukoff, one of the first major American collectors to explore Amazonian Brazil, and whose philanthropy funds many important botanical functions to this day. In addition, Krukoff was the first known collector of the present species.

BRAZIL. AMAZONAS: Barcelos, *Duarte 6958* (RB); Rio Embira (tributary of Rio Tarauaca), 7°30′S, 70°15′W, *Krukoff 4927* (NY); Mpo. Maraa, Rio Japurá, vic. Maraa, Lago Maraa, *Plowman et al. 12211* (MO, INPA); Sitio Fortaleza, 7 km NW of Maraa, *Plowman et al. 12278* (INPA, NY); mouth of Igarape Maraa and Lago Maraa, *Plowman et al. 12380* (NY, INPA); Mpo. Tefe, Lago Tefe, Vila Nogueira, Porto Camanaus, *Byron et al. 621* (MO, INPA); Lago Tefe, NW shore, *Plowman et al. 12442* (MO, INPA).

Anthurium lanjouwii Jonk. & Jonk., Acta Bot. Neerl. 15: 133. 1966. TYPE: Surinam. Emma Mountains, S slope, 850 m, *Daniels & Jonker 1101* (holotype, U). Figure 348.

Terrestrial; stem to 15 cm long; internodes short, 1–1.5 cm diam.; roots moderately dense, spreading, to 25 cm long, the younger roots light brown, villous; cataphylls narrowly triangular, 3.4–5 cm long, persisting semi-intact toward apex, as fibers toward base. *Leaves* with petioles 7–23 cm long, drying 3–7 mm diam., subterete, sulcate adaxially, drying with sharp margins, rounded abaxially; geniculum sharply sulcate, 0.5–1 cm long; blades subcoriaceous, elliptic to ovate-elliptic, acuminate and apiculate at apex, obtuse to rounded or sometimes cuneate at base, 23–36 cm long, 12–19 cm wide, drying yellow-green to yellow-brown; midrib prominently riased on both surfaces, drying angular and paler than surface below; primary lateral veins 6–9 per side, departing midrib at 40–60° angle, moderately straight to the margin, then markedly ascending and merging with the margin or loop-connecting with the next higher vein, raised on both surfaces; tertiary veins drying prominulous below; collective vein lacking or arising below the middle of the blade. *Inflorescences* erect, shorter than leaves; peduncle 17–39 cm long; spathe promptly withering and soon deciduous, green tinged with purple, lanceolate, 2.5–4.5 cm long, 0.7–0.8 cm wide, inserted at ca. 45° angle on peduncle, mucronate at apex, acute at base; spadix purplish brown, weakly tapered, short-stipitate, 5–14 cm long, drying 4–6 mm diam.; flowers rhombic, 2.5–

3.3 mm long, 1.7–2.3 mm wide, the sides smoothly sigmoid parallel to spiral, jaggedly sigmoid perpendicular to spiral; 5–7 flowers visible in principal spiral; tepals matte and brown on drying; lateral tepals 0.8 mm wide, the inner margins rounded, the outer margins bluntly triangular; pistils not at all emergent; stigma linear, slitlike, to 0.8 mm long, stamens emerging in a regular sequence, held just above the tepals in a tight cluster above pistil, inclined over and obscuring the pistil; anthers 4 mm long, 5.5 mm wide; thecae ovoid, moderately divaricate. *Infructescence* unknown.

Anthurium lanjouwii is endemic to Surinam, known only from steep southern slopes of the Emma Mountains, on sandstone and dolomite, at 850 m.

This species is most closely related to *Anthurium bonplandii* and may prove to be only subspecific with that taxon. It differs from that species in being isolated geographically, having more or less elliptic blades and lacking plate-glands or pustules. It is geographically closest to *A. bonplandii* subssp. *guayanum*, which has much larger, oblanceolate to obovate blades with conspicuous dark glandular-punctations.

FRENCH GUIANA. Sommet Tabulaire, 40 km SE of Saül, 650–700 m, *Cremers 6469* (CAY). SURINAM. Emma Mountains, south, sandstone slope, 850 m, *Daniels & Jonker 1101, 1241, 1264* (U).

Anthurium latissimum Engl., Pflanzenr. IV. 23B(Heft 21): 292. 1905. TYPE: Peru. Junín: Prov. Tarma, La Merced, Río Chanchamayo, 1,000 m, *Weberbauer 1939* (holotype, B; isotype, MO-3122266). Figures 167–170.

Terrestrial or epiphytic; stem to 30 cm long, 2–3.5 cm diam.; roots dense, descending, white, fuzzy, short, ca. 3 mm diam.; cataphylls subcoriaceous, lanceolate to hook-shaped, 2-ribbed, 5–11.5 cm long, acute to acuminate at apex, drying reddish brown, persisting semi-intact, eventually as a reticulum of fibers. *Leaves* erect-spreading; petioles 8–48 cm long, 4–12 mm diam., sharply D-shaped to C-shaped, flattened to sulcate and with a medial rib adaxially, the margins sharply to bluntly raised or bluntly acute, rounded to 3–5-ribbed abaxially, the surface pale-short-lineate, sometimes tinged with purple; geniculum paler and thicker than petiole, becoming calloused and minutely transverse-fissured with age, 1–2 cm long; sheath 3–10 cm long; blades subcoriaceous, broadly oblanceolate to obovate-elliptic to broadly elliptic, acute to acuminate at apex, acute to attenuate at base, (26)50–125 cm long, 10.5–36.5 cm wide, broadest at or above the middle, the margins undulate, concave toward base; upper surface semiglossy, dark to medium green, lower surface semiglossy to weakly glossy, moderately paler; midrib above flat to bluntly raised at base, becoming sharply acute toward the apex and paler than surface, below bluntly acute at base, becoming broadly convex to acutely raised toward the apex; primary lateral veins 6–14 per side, departing midrib at 70–90° angle, retrorse to 130° toward the base, ± straight to arcuate ascending to the margin, raised above, bluntly convex below; interprimary veins not visible; tertiary veins weakly raised above, flat and darker than surface below; collective vein arising from near the base or near the apex, prominulous, 2–10 mm from margin. *Inflorescences* erect to spreading; peduncle (10)30–98 cm long, 2–9 mm diam., 1.2–4.6× as long as petiole, green to reddish green, terete; spathe reflexed-spreading, sometimes recurled, subcoriaceous, sometimes reddish, usually green tinged with red or purple (B & K yellow 5/7.5), broadly lanceolate, (3.5)8–12(18) cm long, 1.3–2.5 cm wide, broadest near the base, inserted at 40–60° angle on peduncle, acute to acuminate at apex (the acumen apiculate), acute to rounded at base; spadix olive-green to gray-green to brownish to violet-purple (B & K red-purple 2/2.5), sometimes weakly glaucous, slightly tapered, sessile or stipitate to 2 cm, erect, straight to curved, held at ca. 180° angle from peduncle, 5–13(28) cm long, 4–7 mm diam. midway, 2–4 mm diam. near apex; flowers rhombic to 4-lobed, 2–2.3 mm long, 2 mm wide, the sides smoothly sigmoid to jagged; 7–10 flowers visible in principal spiral, 5–7 in alternate spiral; tepals minutely papillate, matte, white-pustulate; lateral tepals 0.5–0.6 mm wide, the outer margins 3–4-sided, the inner margins weakly curved; pistils papillate, minutely granulose, raised, red-violet to maroon; stigma linear, 0.4 mm long; stamens emerging in a regular sequence, the laterals preceding the alternates by 4–14 spirals, the 3rd stamen preceding the 4th by 5–7 spirals, arranged in a circle around the pistil; anthers pinkish to reddish brown, 0.5–0.7 mm long, 0.5–0.7 mm wide, thecae divaricate; pollen yellow fading to white, yeasty-scented. *Infructescence* with spathe persisting; spadix 9–17 cm long; berries maroon to deep red-violet (B & K red-purple 2/5), obovoid, flattened to depressed at apex, 6.5–7.5 mm long, 5–6 mm diam.; mesocarp transparent, gelatinous; seeds 2 per berry, white tinged with red-violet at base, 4.5–6 mm long, 2–3.5 mm diam.

Anthurium latissimum is endemic to Peru, where it ranges from San Martín to Huánuco, Junín, and

Ayacucho at 500 to 1,800 m in tropical moist, premontane moist, or tropical dry forest life zones.

This species is characterized by its usually long-petiolate blades which are rather abruptly attenuate in the lower third with concave margins, and especially by having the primary lateral veins in the lower part of the blade departing the midrib at a right angle to the midrib, or even markedly retorse toward the base, before arching upwards toward the margins.

Anthurium latissimum is perhaps most closely related to *A. ernestii*, which has generally smaller leaves that lack the retrorse or perpendicular veins, and usually occurs below 500 m.

Younger plants, represented by *Killip & Smith 24612* for example, may have small blades that are scarcely attenuate at the base. They also differ in having a stubbier spadix with only five to six flowers per spiral. Also noteworthy is *Croat 51171*, which dried greenish in contrast to most other, brown-drying material. It differs in no other respect.

While the tepals of most dried collections are at least sparsely papillate, a collection of cultivated origin believed to be this species (*Croat 52230A*) has densely granulose tepals which appear to be paler than those of most other collections.

PERU. Without locality, cultivated at MO: *Croat 52230A* (B, CAS, CM, F, K, M, MO, NY, P, RSA, S, US, USM). AYACUCHO: Huanta–Río Apurimac, Auina, 750–1,000 m, *Killip & Smith 22836* (NY, US). HUÁNUCO: Prov. Leoncio Prado. Tingo María Region, Lima-Tingo María, Km 504, Río Huallaga, 750 m, *Young & Sullivan 807* (MO); Km 478, 1,400 m, *Young & Sullivan 835* (MO); Dtto. Rupa Rupa, E of Tingo María, Cerro Quemado, 800–850 m, *Schunke 10498* (MO). JUNÍN: San Ramón–Oxapampa, 6 km N of turnoff to Satiapo, 700 m, 10°53′N, 75°18′W, *Croat 57727* (AAU, BM, MO, RSA, USM); Prov. Tarma, Tarma–San Ramón, Schunke Hacienda, La Merced, 1,300 m, *Macbride 5678* (F); Tarma–San Ramón, Schunke Hacienda, 1,400–1,700 m, *Killip & Smith 24589, 24612* (NY, US); Río Chanchamayo, La Merced, 1,000 m, *Weberbauer 1939* (B, MO); Río Vitoc, vicinity of Río Chanchamayo, ca. 1,000 m, *Soukup 4405* (US). SAN MARTÍN: Río Huallaga, Tingo María–Huánuco, 20 km from Tingo María, 625–1,100 m, *Allard 21977* (US); Prov. Lamas, Tarapoto–Moyobamba, 10 km NW of Tabalosos, 500 m, 6°15′S, 76°43′W, *Croat 51171* (MO, US); Prov. Mariscal Cáceres, Dtto. Uchiza, Tingo María–Tocache Nuevo, behind Ramal de Aspusana, 25.8 km N of turnoff to Tocache Nuevo from Tingo María–Pucalpa road, 500 m, 9°07′S, 76°03′W, *Croat 57967* (MO).

Anthurium lennartii Croat, sp. nov. TYPE: Ecuador. Loja: Celica–Zapotillo Road, ca. 3 km below Pózul, 1,400 m, *Harling & Andersson 18071* (holotype, MO 2908943; isotype, GB 897-61). Figure 171.

Planta epiphytica; internodia ca. 1.5 cm diam.; cataphyllum persistens in fibris tenuibus; petiolus 7–11.5 cm longus, 5–7 mm diam., D-formatus; lamina oblongo-elliptica, 55–98 cm longa, 10–17.5 cm lata, apice obtusa ad rotundata; pedunculus 20.5–37.5 cm longus, 3–4 mm diam.; spatha 7.5–9 cm longa, 1.5–2 cm lata; spadix lentiter contractus, 7 cm longus, 5–6 cm diam., viridis ad lilicinus; baccae rubentes ad atropurpureae.

Description based on dried material only. Epiphytic; stem ca. 1.5 cm diam.; roots moderately numerous, pale grayish, shortly pubescent, moderately elongate, ca. 2–3 mm diam.; cataphylls subcoriaceous, ca. 10 cm long, light brown, persisting as linear fibers, soon deciduous. *Leaves* with petioles 7–11.5 cm long, 5–7 mm diam., D-shaped, with the margins sharply raised adaxially, probably 2–3-ribbed abaxially; geniculum slightly thicker than petiole, sometimes fissured transversely, 0.8–1.5 cm long; sheath 3.5–5.5 cm long; blades subcoriaceous, oblong-elliptic, obtuse to semi-rounded at apex (the acumen shortly apiculate), obtuse to narrowly rounded at base, 55–98 cm long, 10–17.5 cm wide, broadest at or near the middle, both surfaces matte, green to yellowish; midrib convexly raised above, somewhat acute at base, becoming prominently convex toward the apex below; primary lateral veins 16–23 per side, departing midrib at (40)55–85° angle, arcuate to the collective vein, convexly raised above and below and paler than surface; interprimary veins moderately numerous, raised on both surfaces; tertiary veins weakly raised above and below; collective vein arising from the base or near the base, less prominent than primary lateral veins, raised above and below, 2–7 mm from margin. *Inflorescences* with peduncle 20.5–37.5 cm long, ca. 3–4 mm diam., 2.9–3.7× as long as petiole, greenish to yellowish green, probably terete; spathe apparently spreading, subcoriaceous, green, broadly linear to linear-lanceolate, 7.5–9 cm long, 1.5–2 cm wide, broadest near the base, abruptly acuminate at apex (the acumen inrolled), acute at base; stipe 13 mm long in front, 3 mm long in back; spadix green, weakly tapered, 7 cm long, 5–6 mm diam. near base, 4 mm diam. near apex, broadest at the base; flowers rhombic to 4-lobed, 1.6–1.9 mm long, 1.5–1.8 mm wide, the sides usually jaggedly sigmoid, sometimes smoothly sigmoid; 6–8 flowers visible in principal spiral, 5–6 in alternate spiral; tepals roughened; lateral tepals 1–1.3 mm wide, the inner margins erose, broadly convex, the outer margins 2-sided; pistils exposed, yellowish; stigma slitlike, dark, ca. 0.4 mm long; anthers 0.5–0.7 mm long, 0.7–0.9 mm wide; thecae ovoid to oblong-ovoid, 0.3–0.4 mm wide, not divaricate. *Infructescence* with spathe

persisting; spadix 15.5–26 cm long, 2.2–2.5 cm diam., with tepals becoming enlarged and conspicuous, often purplish; berries red to dark purple, after rehydration ovoid to ovoid-ellipsoid, acute to ± rounded at apex, 6.3–8.5 mm long, 3.7–4.3 mm diam.; pericarp translucent with pale, linear raphide cells; mesocarp gelatinous, translucent, reddish; seeds 1–2 per berry, yellowish, ovoid to oblong-ovoid, flattened, 3–3.5 mm long, 2–2.7 mm diam., 1–1.5 mm thick, enveloped by gelatinous substance.

Anthurium lennartii is endemic to southern Ecuador, where it occurs in Loja Province, in lower montane moist to premontane dry forest life zones, at 1,400 to 2,700 m. It is expected in adjacent Peru.

This species is characterized by its greenish-drying, oblong-elliptic blades that are obtuse to narrowly rounded at the apex, its basally originating collective vein running fairly close to the margin, its moderately numerous primary lateral veins, and by its weakly tapered spadix. Unique features of *Anthurium lennartii* are its conspicuously accrescent, purplish tepals and red to purple berries.

Anthurium lennartii appears to be superficially similar to *A. manabianum*. The two species share in common general blade color on drying and spadix and spathe shape, but differ in blade shape and stipe length, which is up to 3 cm in *A. manabianum*. An important difference between these species is their distribution, with *A. lennartii* occurring in southern Andean Ecuador and *A. manabianum* in the coastal part of the country, in Manabí Province at 450 m.

Anthurium lennartii is also similar in its appearance to *A. sodiroanum* Engl., a member of sect. *Xialophyllium*, which vaguely resembles other species of sect. *Pachyneurium*. *Anthurium lennartii* differs from *Anthurium sodiroanum* by having shorter nodes, collective vein running closer to the margin, more prominent primary lateral veins, a slightly broader spathe, and an elevational range to 2,700 m.

The new species is named in honor of Lennart Andersson of the University of Göteborg, who collected, with Gunnar Harling, all known species of *A. lennartii*.

ECUADOR. LOJA: 8 km W of Celica on road to Alamor, 2,000 m, *Harling & Andersson 22159* (GB); Celica–Gauachanama, Km 8, 2,700 m, *Harling & Andersson 22302* (GB); Celica–Zapotillo, 3 km below Pózul, 1,400 m, *Harling & Andersson 18071* (GB, MO).

Anthurium leonianum Sodiro, Anales Univ. Centr. Ecuador 17(123): 256. Jan. 1903. TYPE: Ecuador. Imbabura: W slopes of Volcán Cotatachi, 0°22′N, 78°20′W, *Sodiro s.n.* (holotype, B; isotype, QPLS). Figures 172–174.

Terrestrial on rocky slopes; stem to 3 cm diam.; roots spreading-descending, whitish, appearing pubescent when fresh, thick, rather short, prominently tapered; cataphylls subcoriaceous, lanceolate, longer than petioles, acuminate at apex, drying brown, persisting as fine linear fibers. *Leaves* erect-spreading to spreading; petioles 5–22 cm long, 10–15 mm diam., D-shaped, flattened and with a medial rib to broadly and sharply sulcate adaxially with the margins prominently raised, 5–8-ribbed abaxially, the surface pale-speckled; geniculum thicker and paler than petiole, 1–1.5 cm long; sheath 6–8 cm long; blades coriaceous, obtuse to acute at apex, rounded to acute at base, (23)43–101 cm long, 8–29 cm wide, broadest at or near the middle, the margins prominently undulate; upper surface matte to semiglossy, dark green, lower surface matte to weakly glossy, paler, both surfaces drying yellowish green; midrib flat at base, becoming acutely raised toward the apex and conspicuously paler than surface above, prominently higher than broad at base, becoming acutely raised toward the apex below; primary lateral veins 10–15 per side, departing midrib at 45–60° angle, ascending ± straight to near margin, then arcuate-ascending and merging with margin, prominently convexly raised above and below; tertiary veins prominulous when dried above and below; collective vein arising from near the apex, raised above and below when dried, usually less than 5 mm from margin. *Inflorescences* ± erect, equaling or longer than leaves; peduncle 46–91 cm long, 10–17 mm diam., 4–5× as long as petiole, subterete to 1-ribbed; spathe reflexed, coriaceous, green, long-lanceolate, 29–35 cm long, 2–5 cm wide, broadest near base; spadix dark purple (pre-anthesis), becoming greenish brown, long-tapered, 23.5–42 cm long, 10–12 mm diam. near base, 5–7 mm diam. near apex; flowers 4-lobed, 2.2 mm long, 1.5 mm wide; 14–15 flowers visible in principal spiral, 7–9 in alternate spiral; tepals weakly and minutely papillate; pistils weakly emergent; anthers ca. 0.5 mm long. *Infructescence*, 2.5–3 cm diam.; berries dark purple at apex, obovoid.

Anthurium leonianum is endemic to Ecuador in the province of Imbabura from 900 to 1,500 m, in lower montane dry or premontane moist forest life zones.

This species is recognized by its thick, erect to spreading leaves which dry yellow-green, its petioles which are sharply sulcate adaxially and 5–8-ribbed abaxially, and by its long-tapered, deep purple spadix which becomes greenish brown at anthesis. It is also reported to have deep purple berries.

Anthurium leonianum might be confused with *A. dombeyanum*, which, in Ecuador, occurs only in the provinces of Loja and Tungurahua (only two collections are known from the latter province). *Anthurium dombeyanum* differs mainly in having the petioles rounded abaxially. In addition, the leaf blades of *A. leonianum* are conspicuously yellow-green on drying, while in *A. dombeyanum* they are usually brownish or dull grayish green. The spadix of *A. dombeyanum* is generally shorter than that of *A. leonianum*.

Anthurium leonianum also bears some resemblance to two species from central Colombia, *A. glaucospadix* and *A. caucavallense*. Both have, at least at times, yellowish green leaf blades on drying, though the color more closely approaches that of some specimens of *A. dombeyanum*. Although the cataphylls of the type specimen of *A. leonianum* at Berlin appear to be hooked and refolded, they are straight and lanceolate on living collections from the same area. It is here believed that the cataphylls of the type specimen are so shaped because of the way it was prepared. This character, along with the lower angle of the primary lateral veins (45–60 vs. 50–90°) and peduncle-petiole ratio (peduncles 4–5 vs. 1–2 times longer than the petioles in *A. leonianum*), serve to distinguish this species from *A. caucavallense*. *Anthurium glaucospadix* also differs in having the primary lateral veins depart the midrib at a broad angle, as well as in having a bluish green, glaucous spadix and red berries.

The name *Anthurium leonianum* was used in the Flora of Río Palenque (Dodson & Gentry, 1978), based on *Dodson & Tan 5389*, but that collection represents a new and unrelated species, *A. sparreorum*, described in the present treatment. The latter species has a thinner blade with the collective veins arising at the base and running close to the margin, whereas *A. leonianum* has a coriaceous blade with the collective vein arising from one of the primary lateral veins in the upper ¼ of the blade. A character that may be used to distinguish the two immediately is the number of primary lateral veins per side (10–15 in *A. leonianum* vs. (15)20–30 in *A. sparreorum*). *Anthurium sparreorum* is known from lower elevations, generally around 200–300 m in premontane wet forest.

ECUADOR. IMBABURA: Ibarra–Lita, 1,500 m, *Cobb 21 E* (MO, QCA); Salinas–Lita, 900–1,000 m, 0°45′N, 78°15′W, *Juncosa 2262* (K, MO); Tercer Paso, on San Lorenzo RR, 1,100 m, *Madison et al. 4960* (MO, SEL); Volcán Cotacachi, W slopes, *Sodiro s.n.* (B, QPLS); Río Meta, Ibarra–Lita, E of La Carolina, border of Carchí Prov., 1,090 m, *Croat 38986* (MO).

Anthurium lindmanianum Engl., Bot. Jahrb. Syst. 25: 367. 1898. TYPE: Brazil. Mato Grosso: Cupim near Palmeiras, *Lindman 2455 1/2* (lectotype, S). Figures 175–177.

Anthurium douradense Rizzo, Rev. Goiana Med. 16: 31–33. 1970. TYPE: Brazil. Goias: Serra Dourada, *Rizzo 4532* (holotype, UFG; isotype, RB).

Terrestrial or epilithic, rarely epiphytic; stem frequently creeping over ground, 1–5 cm diam.; roots moderately dense, descending, fuzzy, drying 2–4 mm diam.; cataphylls subcoriaceous, lanceolate, 2–9(15) cm long, acute to acuminate at apex, green, drying reddish brown, persisting ± intact or as coarse linear fibers. *Leaves* erect-spreading; petioles (2)11–57(65) cm long, (2)8–18 mm diam., bluntly to sharply D-shaped, flattened to slightly sulcate adaxially, rounded abaxially, the surface pale-speckled; geniculum slightly paler and thicker than petiole, (0.2)0.8–2 cm long; blades coriaceous to subcoriaceous, oblanceolate to broadly elliptic, acute to obtuse to short-acuminate at apex, cuneate-attenuate to obtuse to rounded, rarely shallowly cordate at base, (14)20–84 cm long, (4.2)12–29(34) cm wide, broadest usually above the middle, the margins usually flat, sometimes broadly undulate; upper surface glossy to semiglossy, medium green (B & K green 2/2.5), lower surface matte, paler; major veins sometimes paler on both surfaces; midrib convexly raised above, prominently and acutely raised below (about as high as broad); primary lateral veins (4)7–10(14) per side, departing midrib at (30)40–60(80)° angle, arcuate-ascending to the margin or to the collective vein, raised, sometimes becoming sunken toward margin above, raised below; tertiary veins weakly etched, and sometimes concolorous above, prominulous and darker below, conspicuously raised on both surfaces when dried; collective vein arising from about the middle to near the apex of the blade or absent, sunken above, weakly raised below, 5–13 mm from margin. *Inflorescences* erect to spreading, equaling or longer than leaves; peduncle (15)35–134 cm long, (1)2–12 mm diam., 1.3–2.3(14.6)× as long as petiole, terete; spathe spreading to reflexed, sometimes recurled, subcoriaceous, withering and/or deciduous, yellow-green (B & K yellow-green

8/10), lanceolate, (3)5–17 cm long, (0.5)1–2 cm wide, broadest near the base, inserted at 20–40° angle on peduncle, long-acuminate at apex (the acumen ca. 3 mm long), acute to obtuse at base; spadix pinkish to dull brownish olive-green to dark red or purplish violet, oblong, weakly tapered, sessile or stipitate to 4 cm, erect, (1.5)4–12(20) cm long, 3–7 mm diam. midway, 1.5–4 mm diam. near apex, moderately tapered; flowers 4-lobed, 1.8–3 mm long, 1.2–2.7 mm wide; (2)4–9 flowers visible in principal spiral, 4–10 in alternate spiral; tepals matte, minutely papillate; lateral tepals 0.9–2.2 mm wide, the inner margins straight to broadly rounded, sometimes minutely and unevenly erose, the outer margins 2–5-sided; pistils not emergent before anthesis, slightly raised at anthesis, caviform with erect, reddish margins; stigma linear becoming circular, 0.2–0.3 mm long; lateral stamens preceding the alternates by 2–16 spirals, the 3rd stamen preceding the 4th by 7–10 spirals; anthers 0.4–0.6 mm long, 0.4–0.7 mm wide, inclined over and obscuring the pistil; thecae ovoid-ellipsoid, not divaricate. *Infructescence* with spathe deciduous; spadix normally more than 15 cm long, bearing berries in the basal portion only; berries dark purple to dark red toward the apex, white below, obovoid, "hollow" when rehydrated, 7–9 mm long, 4–6 mm diam.; seeds 1–2 per berry, 5.5–6.8 mm long, 3–3.5 mm diam., 2–2.3 mm thick, weakly apiculate at both ends, pale-punctate.

Anthurium lindmanianum is known from Brazil in the states of Mato Grosso, Rondônia, Goiás and in the southern and central eastern parts of Pará at 90 to 1,000 m. It grows terrestrially in sandy soil, frequently along stream banks, among or on sandstone rocks, in gallery forest and scrub.

This species is recognized by its broadly elliptic or sometimes oblanceolate blades, which are rounded to abruptly acuminate at the apex, by its long-pedunculate inflorescence, and by its berries, which are purple at the apex and whitish at the base. It is also distinguished by its stem creeping over the surface of the ground and by its leaves being erect from the apex of the stem. The stem may even be subterranean. In cultivation, the species grows best when given direct access to water, e.g., when growing on a large brick placed in a pool of water. The appressed stem adheres closely to the brick (above the water line) in this situation.

Anthurium lindmanianum is most easily confused with *A. bonplandii* subsp. *bonplandii*, which occurs in the same state of Brazil (Pará). Typical specimens of *A. bonplandii* from Pará, all collected north of the Rio Amazonas, mostly differ in having conspicuous, dark brown plate glands on the undersurface of the leaf blades, and prominently raised tertiary venation on both leaf blade surfaces on drying. In contrast, the tertiary venation of *A. lindmanianum* is inconspicuous on the upper surface and generally less conspicuous on the lower surface on drying, and dark brown (or colorless) glandular punctations are normally not present and are not conspicuous where observed. In Pará, *A. lindmanianum* occurs in the area of the Serra dos Carajas in the central eastern part of the state, and in the Serra do Cachimbo (including the immediate lowlands to the north, i.e., the Rio Cururú) in the southwest. Thus, the species appears to prefer upland areas, a trend which continues toward the south, where it is more prevalent.

A few collections from Pará deserve mention, being rather markedly different from typical material and possibly meriting subspecific recognition once the taxon is better represented in herbaria by collections from this area. These collections, *Berg & Henderson 493*, *Bockerman 248*, *Sperling et al. 5658*, and *Secco et al. 136*, are all smaller than average for the species in all aspects and have a prominently stipitate spadix. In addition, the peduncle may be up to 14.6× larger than the petiole (vs. 1.3–2.3 times for typical material), and the spadix of two of these collections is reported as "black."

BRAZIL. Cultivated at Munich Bot. Gard., *Bogner 586* (MO); cultivated by Burle-Marx, *Croat 57174* (MO); cultivated at Tropic World, San Diego, California, *Croat 57157* (MO). GOIÁS: Rio Araguaia, 6 km NW of Piranhas, 700 m, *Irwin et al. 17703* (IAN, K, MO); Serra do Caiapo, 12 km S of Caiaponia, near small creek, 720 m, *Hutchison 8505* (MO); 48 km S of Caiaponia, 800–1,000 m, 17°12′S, 51°47′W, *Irwin & Soderstrom 7239* (MO, SEL), *Prance & Silva 59634* (K, NY); Serra Dourada, *Rizzo 4532* (RB, UFG); 1.3 km NW of junction with road to Mossâmedes on GO 070 from Goiania to Goías, 750–800 m, 15°57′S, 50°02′W, *Thomas et al. 5778* (NY). MATO GROSSO: 30 km ENE of Barra do Garcas, 450 m, *Anderson 9785* (RB); Chapada dos Guimaraes, above Veu da Noiva, 720 m, *Prance et al. 19164* (U); 5 km E of Chapada dos Guimaraes, road to EMBRATAL, 720 m, *Prance et al. 19375* (NY); 270 km N of Xavantina, 12°54′S, 51°22′W, *Gifford 146* (NY); Cerrado–Pantanal, Matas de Transição, 600 m, *Martinelli 366* (K); Serra Itapirapuan, *Lindman 2407 1/2* (cited by Engler (1898) as *2455 1/2*) (B, S); Araguaia, direção Rondopolis, *Hutchison 8548* (UEC); Fazenda Cachimbo, *Cordeiro 1087* (MG, US); base camp, 12°49′S, 51°46′W, *Harley et al. 10631* (K); Xavantina–São Felix, 12°54′S, 51°52′W, *Ratter et al. 960, 966* (K); Xavantina, 12°54′S, 51°22′W, *Gifford 145, 146* (K); Ponte de Pedra, *Hatschbach & Koczicki 33205* (K); Cupim, near Palmeiras, *Lindman 2455 1/2* (S); Rio Juruena, Cachoeira Misericordia, *Rosa & Santos 1998* (MG, MO, NY); Serra Ricardo Franco, 700–800 m, 15°S, 60°W, *Windisch 1623* (K); Serra do Roncador, 84–85 km N of

Xavantina, 550 m, *Hunt 5800* (K), *Hunt & Ramos 5740* (K, NY), *Irwin et al. 16446* (GH, IAN, MO, TEX); Mpo. Jauru & Pontes e Lacerda, 38 km SE of Pontes e Lacerda on BR 174 to Cáceres, 15°27′S, 59°04′W, *Thomas et al. 4694* (NY); Mpo. Luciaria, 43 km S of Pto. Alegre do Norte, 1–5 km W of BR158, 11°17′S, 51°45′W, *Thomas et al. 4440* (MO); Mpo. Rondonopolis, Serra da Petrolina, *Hatschbach 34125* (K). PARÁ: Maraba, Alto da Serra, *Secco et al. 136* (MO); Rio Cururú, canal SE of Missão Cururú, Alto Tapajós, 140 m, 7°35′S, 57°31′W, *Anderson 10602* (NY); 2 hours downstream from Missão Cururú, Mouro, Alto Tapajós, 100–200 m, 7°15′S, 57°55′W, *Anderson 11080* (COL, K, MO, NY, U); Tapajós, *Rosa & Santos 1906* (MG, MO, NY); Serra do Cachimbo, Cachimbo, 500–600 m, 9°20′S, 54°53′W, *Bockermann 248* (UB), *Pereira 1821* (RB); Serra dos Carajás, Serra Norte, AMZA exploration camp, 600 m, 6°00′S, 50°15′W, *Berg & Henderson 493* (F, GH, INPA, MG, RB, US, WIS); 2 km W of AMZA Exploration Camp N-5, 700 m, 6°04′S, 50°08′W, *Sperling et al. 5658* (MG, MO); 20 km NW of Serra Norte mining camp, less than 500 m, 5°55′S, 50°26′W, *Daly et al. 1697* (INPA, MG, MO); Serra Norte, Maraba, Clareira N-1, *Cavalcante & Silva 2631* (MG), *Silva et al. 1631, 1866* (MG); Mpo. Itaituba, Serra do Cachimbo, 5 km from Cachimbo airport, along Rio Formiga, 500–600 m, 9°23′S, 54°55′W, *Silva et al. 135* (NY, INPA). RONDÔNIA: ca. 35 km WSW of Ariquemes, Mineraceo Taboca at Massangana, 10°02′S, 63°20′W, *Zarucchi et al. 2650* (F, INPA, MG, MO, NY, RB, US); 4 km from Ariquemes, BR-364, 200–500 m, 9°55′S, 63°06′W, *Vieira et al. 548* (MG, MO, NY).

Anthurium linguifolium Engl., Pflanzenr. IV. 23B(Heft 21): 162. 1905. TYPE: Ecuador. Manabí: between El Recreo and Agua Amarga, *Eggers 15530* (lectotype, B; isolectotypes, F, K). Figures 178, 180.

Terrestrial; stem to 19 cm long, ca. 1 cm diam.; roots dense, ascending, green to whitish, pubescent to smooth, short, 1–1.5 cm long, 5–6 mm diam.; cataphylls subcoriaceous, linear-lanceolate, 3–10.5 cm long, obtuse to acute or acuminate at apex, drying reddish brown (B & K yellow-red 4/10), persisting ± intact, splitting at base. *Leaves* erect-spreading; petioles 4–7 cm long, 5–7 mm diam., erect-spreading, subtriangular, convexly raised to obtusely ribbed, sometimes broadly sulcate adaxially, the margins sharply raised, somewhat rounded and sharply 1-ribbed abaxially, conspicuously swollen to 14 mm diam. at base; geniculum slightly paler and conspicuously thicker than petiole, 0.5–2 cm long; blades subcoriaceous, oblong-linear, acute, sometimes apiculate at apex, acute to rounded at base, 25–85 cm long, 2.5–6.5 cm wide, broadest at or near the middle, the margins broadly and shallowly undulate; upper surface matte to semiglossy, medium green, lower surface matte, conspicuously paler; midrib above obtusely raised at base, becoming sharply and acutely raised and higher than broad toward the apex, pale-speckled, slightly paler than surface, below acute throughout, paler and more yellowish than surface; primary lateral veins 8–15 per side, departing midrib at 30–60(–70)° angle, not well distinguished from interprimary veins, slightly arcuate to the margin, weakly sunken to weakly raised in shallow grooves, rather obscure above; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins obscure above, conspicuously darker than surface below, prominulous on both surfaces when dried; collective vein usually arising from near the apex, sometimes from near the base, obscure above, equally as prominent as interprimary veins below, 1–7 mm from margin. *Inflorescences* erect-spreading to spreading, shorter than or equaling leaves; peduncle 38–57 cm long, 4 mm diam., 7.6–19(38)× as long as petiole, green, terete; spathe spreading to reflexed-spreading, coriaceous, yellow-green, sometimes tinged with purple abaxially (B & K yellow-green 5/7.5), narrowly lanceolate, 7–8.5 cm long, 0.8–1.5 cm wide, broadest near the base, inserted at 45° angle on peduncle, acuminate at apex (the acumen inrolled), obtusely rounded at base; spadix glaucous, dull lavender-purple (B & K purple 5/2.5), sessile, slightly tapered, cylindroid, erect, 5–8.2 cm long, 7–9 mm diam. near base, 4–6 mm diam. near apex, broadest at the base; flowers 4-lobed, 2.1–2.6 mm long, (1.5)2.4–3 mm wide, the sides weakly sigmoid; (4)7–9 flowers visible in principal spiral, (3)5–7 in alternate spiral; tepals matte; lateral tepals 0.8–1.4 mm wide, the inner margins weakly concave to slightly rounded, the outer margins usually 2-, sometimes 3–4-sided; pistils emergent, bright green (B & K yellow 5/2.5); stigma ellipsoid, 0.3–0.4 mm long; stamens emerging in a regular sequence from the base, the laterals preceding the alternates by 9 spirals, the 3rd stamen preceding the 4th by 3 spirals, borne at edge of tepals in a circle around the pistil; anthers straw-colored (B & K yellow-red 9/10), 0.6 mm long, 0.8 mm wide; thecae ovoid, slightly or not divaricate; pollen pale yellow (B & K yellow 9/2.5), sweetly scented at anthesis. *Infructescence* with persistent spathe; fruits not seen.

Anthurium linguifolium is known from only two collections made in coastal Ecuador in Manabí province, between Bahía de Caraquez and Canoa, near sea level in a very dry tropical forest life zone.

This species is characterized by its linear-oblong, weakly undulate blades, short petioles, rather elongate stem with short, more or less erect roots throughout its length (above ground) and by its glaucous, dull lavender-purple spadix.

The closest ally of *A. linguifolium* is *A. barclayanum*. The latter differs in greenish (rarely violet-purple) spadix, much larger size, longer petioles and oblanceolate blades. *Anthurium barclayanum* is sympatric with the present species at one locality at least, but they occur in very different habitats. The first is epiphytic, the second terrestrial in open areas. In addition, the ratio of peduncle to petiole length is much greater in *A. linguifolium* (7.6–19(38) vs. 3.5–6(9)).

ECUADOR. MANABÍ: 6 km N of Bahía de Caraquez, 3–4 km E of ocean, 50 m, 0°30′S, 80°22′W, *Croat 50697* (K, MO, NY, QCA, US); El Recreo–Agria Amarga, 0°29′S, 80°27′W, *Eggers 15530* (B, F, K, NY).

Anthurium llewelynii Croat, sp. nov. TYPE: Peru. San Martín: Prov. Tarapoto, Río Mayo, near Cumumbigue, 6 km S of Tarapoto–Moyobamba road at Km 15, 350 m, 6°23′S, 76°39′W, *Croat 51092* (holotype, MO 2819899; isotypes, B, K, M, NY, RSA, SEL, US, USM). Figures 181, 183–185.

Planta terrestris; internodia brevia, 2.5–4 cm diam.; cataphyllum lanceolatum, persistens in reticulum fibrarum; petiolus (5)21–40 cm longus, 3–7 mm diam., adaxile complantus, abaxile rotundatus; lamina oblanceolata ad anguste oblanceata aut elliptica, (29)50–110 cm longa, (5)7–15(20) cm lata, base plerumque abrupte rotundata vel subcordata; nervis primariis lateralibus 4–12 utroque; pedunculus 23.5–75 cm longus, 3–5 mm diam.; spatha lanceolata aut ovato-lanceolatae, 5–9 cm longa, 1--2.5 cm lata, viridis; spadix leviter contractus, 3.6–9 cm longus, 5 mm diam., olivaceus rubellus; baccae atropurpureae, globoso-obovoidae, 3–5 mm diam.

Usually terrestrial, rarely epiphytic; stem creeping, to 20 cm long; internodes short, 2.5–4 cm diam.; roots numerous, dense, descending, whitish, velutinous, 4–5 mm diam.; cataphylls subcoriaceous, lanceolate, 3–7 cm long, acute to acuminate at apex, drying brown (B & K yellow 3/7), persisting as a reticulum of fibers. *Leaves* erect-spreading to spreading; petioles (5)12–40 cm long, 3–8 mm diam., erect, sharply D-shaped, flattened to slightly convex adaxially, rarely with a medial rib, the margins sharply raised, rounded abaxially; geniculum paler than petiole, becoming calloused with transverse fissures, conspicuously thicker than petiole, 0.5–2 cm long, sometimes extending beyond leaf base up to ⅓ its length; sheath 2–6 cm long; blades subcoriaceous, oblanceolate to narrowly oblanceolate or elliptic, acute to acuminate at apex, narrowing toward the base, ending abruptly, obtuse to rounded or shallowly cordate at base, (29)50–110 cm long, (5)7–15(20) cm wide, broadest at or above the middle, the margins moderately to broadly undulate; upper surface glossy to semiglossy, occasionally matte, dark to medium green (B & K green 3/7.5), lower surface matte to semiglossy, considerably paler; midrib pale-speckled, conspicuously to scarcely paler than surface, broadly rounded-raised at base, becoming acutely angled toward the apex above, broadly rounded-raised to bluntly angled and slightly paler than surface below; primary lateral veins 4–12 per side, departing midrib at 35–90° angle (rarely retrorse to 110°), arcuate-ascending to the margin, convexly raised and paler than surface above, less prominently raised and darker than surface below; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins obscure; collective vein arising from near the base or in the upper third of the blade, weakly raised above and below, 3–19 mm from margin. *Inflorescences* erect to spreading; peduncle 23.5–75 cm long, 3–5 mm diam., equaling to 5× as long as petiole, green to brownish green, pale-speckled, terete to subterete; spathe spreading to reflexed, coriaceous to subcoriaceous, green, sometimes tinged with red at margins, lanceolate to ovate-lanceolate, 5–9 cm long, 1–2.5 cm wide, broadest near the base, inserted at 45–60° angle on peduncle, abruptly acuminate to acute at apex (the acumen inrolled), acute at base; spadix reddish olive-green, sessile, cylindroid, slightly tapered, erect or slightly curved, 3.6–9 cm long, 5 mm diam. midway, 3–4 mm diam. near apex; flowers rhombic to 4-lobed, strongly scented like rotting fruit, 1.5–3 mm long, 2–2.4 mm wide, the sides jaggedly sigmoid to straight; 4–8 flowers visible in principal spiral, 5–7 in alternate spiral; tepals matte, sparsely white-punctate, densely papillate; lateral tepals 0.6–0.8 mm wide, the inner margins straight to broadly convex, the outer margins 2–4-sided; pistils weakly raised, olive-green to maroon; stigma linear-oblong, caviform, 5 mm long; stamens emerging in a scattered pattern from the base, the laterals preceding the alternates by up to 17 spirals, the 3rd stamen preceding the 4th by 13 spirals, arranged in a circle around the pistil; anthers pinkish to yellow tinged with pink, 0.3–0.6 mm long, 0.5–0.9 mm wide; thecae oblong-ovoid, slightly divaricate; pollen yellow fading to white. *Infructescence* spreading-pendent; spadix 11–18 cm long, 1–1.3 cm diam.; berries dark purple (B & K red-purple 2/2.5), globose-obovoid to subglobose, truncate at apex, 5 mm long, 3–5 mm diam.; pericarp moderately thickened; mesocarp gelatinous, with raphide cells; seeds 1–2 per berry, brownish purple, oblong-ellipsoid, 4–5 mm long, 2.1–2.5 mm diam., 1.5–

2 mm thick, with a gelatinous appendage at both ends.

Anthurium llewelynii is endemic to Peru, known principally from an area of tropical dry and tropical moist forest in the vicinity of Tarapoto, at 130 m, and also in the vicinity of Tingo María in the Department of Huánuco to 750 m. The species is terrestrial, usually growing in sandy soil along streams, on exposed roadbanks, in shrub forests, or on rocky cliffs above riverbanks.

This species is characterized by its creeping stem, its comparatively long, sharply D-shaped, erect petioles, the usually markedly arching-spreading, narrowly oblanceolate blades (2.2–3.5, averaging 2.8× longer than the petioles) which are usually abruptly and narrowly rounded to shallowly cordate at the base, as well as by the more or less green, moderately short, bluntly tapered spadix and dark purple fruits.

Anthurium llewelynii is not easily confused with any other species growing in the same area and habitats in which it occurs. Only *A. plowmanii* shares similar dry forest habitats in this region, but that species differs in having a peduncle equal to or shorter than the spadix, and a deeply sulcate petiole.

Anthurium tarapotense also occurs in the region, but occurs at slightly higher elevations (360–530 m) in a premontane moist forest life zone. It differs in being less robust and having a generally broader, short-petiolate blade which is attenuate at the base.

It is of interest that individuals of *A. llewelynii* brought into cultivation and grown in more mesic and crowded conditions may develop blades that are narrowly acute at the base, rather than the more characteristic narrowly rounded to subcordate condition. Compare, for example, vouchers prepared in the field and vouchers made from greenhouse plants, respectively, of *Croat 51092*.

Anthurium llewelynii is named in honor of Llewelyn Williams, who collected extensively in the Tarapoto area for the Field Museum in December 1929.

CULTIVATED. Originally from Selby 81-76-1, *Croat 57212* (B, MO). PERU. HUÁNUCO: Prov. Leoncio Prado, Tingo María Region, Río Huallaga, 750 m, *Croat 21086* (MO); Río Huallaga, near bridge and road to Monzón, 675 m, 9°15′S, 75°59′W, *Croat 50981* (MO, NY, RSA, US). SAN MARTÍN: Juanjui–Tarapoto, 35 km S of Tarapoto, 130 m, 6°46′S, 76°21′W, *Croat 58082* (AAU, CAS, CM, GH, K, MO, NY, USM); El Abra, 29 km S of Tarapoto, 450–540 m, 6°40′S, 76°20′W, *Gentry & Smith 45014, 45091A* (MO); Morales, W of Tarapoto, 360–900 m, *Williams 5721* (F); Tarapoto, 350 m, *Williams 5737, 6625* (F); Tarapoto–Yurimaguas, Km 5, *Kennedy 3545A* (ex cult.; = *Plowman 13300*) (F); Río Mayo, 6 km S of Tarapoto–Moyobamba road at Km 15, Cunumbigue, 350 m, 6°23′S, 76°39′W, *Croat 51092* (AAU, B, CM, DUKE, ENCB, IBE, JBGP, K, KYO, L. LE, M, MO, NY, RSA, SAR, SEL, TEX, US, USM); Puente Colombia–Shapaja, 280 m, *Plowman 6018* (GH); Río Shilcayo trail to Boca Toma del Shilcayo, N of Tarapoto, 400 m, 6°30′S, 76°22′W, *Knapp & Alcorn 7336* (K, MO); Dtto. Tarapoto, Tarapoto–Yurimaguas, km 13, 750–1,000 m, *Rimachi 5782* (MO).

Anthurium loretense Croat, sp. nov. TYPE: Peru. Loreto: Prov. Maynas, Dist. Iquitos, Río Momón and Quebrada Momoncillo, 1 km from the Río Nanay, 200 m, *Croat 51226* (holotype, MO 2813874-80; isotypes, B, CAS, DUKE, F, K, NY, US, USM, VEN). Figures 17, 182, 186.

Epiphytic; stem 15–50 cm long, (1)2.5–5 cm diam.; roots dense, spreading-ascending to spreading-descending, green-gray to whitish, puberulent to smooth, slender, ca. 1.5–7 cm long, 5–6 mm diam.; cataphylls subcoriaceous, sometimes coriaceous, 4–6 cm long, hook-shaped, sometimes cucullate at apex, green, drying brown (B & K yellow 4/5), persisting with apex remaining intact and as a reticulum of fibers at base. *Leaves* erect to spreading; petioles 2.5–10(16) cm long, 6–20 mm diam., ± D-shaped to quadrangular, flattened to sulcate with a medial rib and the margins sharply raised adaxially, 3–8-ribbed abaxially; geniculum slightly thicker than petiole, prominently fissured transversely with age, 0.7–3 cm long; sheath 2–8 cm long; blades coriaceous to subcoriaceous, obovate to oblanceolate to elliptic or sometimes spathulate, acute to obtuse at apex (the acumen apiculate), usually abruptly rounded to shallowly cordate, sometimes truncate or acute to attenuate at base, (36)56–120(168) cm long, 30–50(62) cm wide, broadest usually above the middle, the margins broadly undulate; upper surface semiglossy, dark to medium green (B & K yellow-green 4/7.5), lower surface semiglossy to sometimes matte, slightly paler; midrib flat to obtusely raised at base, becoming sharply acute toward the apex above, slightly paler than surface, acutely raised at base, becoming convexly raised toward the apex below; primary lateral veins 10–21 per side, departing midrib at (20)30–60° angle, ± straight to the margin, prominently raised above, slightly paler than surface, prominently convexly raised near the midrib below, becoming acutely raised toward the margin; interprimary veins obscure on both surfaces, promi-

nulous when dried; reticulate veins obscure above, darker than surface below; collective vein arising in the upper third of the blade or absent, flat to weakly sunken above, 4–10(15) mm from margin. *Inflorescences* spreading to spreading-pendent, shorter than leaves; peduncle 25–80 cm long, (2)4–7 mm diam., 4–12(20)× as long as petiole, green to green tinged with maroon or purple-violet, terete; spathe erect to spreading-reflexed to recurled, coriaceous, occasionally subcoriaceous, green heavily tinged with maroon (B & K red-purple 2/7.5), lanceolate to oblong-linear, 5.5–24(35) cm long, 1.2–3m wide, broadest near the base, inserted at 75-80° angle on peduncle, obtuse to long-acuminate at apex, acute to weakly decurrent at base; stipe 3–11 mm long in front, ca. 1 mm long in back; spadix maroon to reddish violet (B & K red-purple 3/10), cylindroid, scarcely to long-tapered, weakly curved, 7.5–28 cm long, 6–11 mm diam. near base, 2–6 mm diam. near apex; flowers square or rhombic to 4-lobed, 1.3–2.1 mm long, 1.3–2.4 mm wide, the sides smoothly to jaggedly sigmoid; 7–13 flowers visible in principal spiral, 5–9 flowers visible in alternate spiral; tepals matte, densely and minutely papillate, with few droplets; lateral tepals 0.6–1 mm wide, the inner margins straight to broadly convex, the outer margins 2–4-sided; pistils emergent, not raised, purple to reddish; stigma linear, purplish violet, 0.3–0.7 mm long; stamens emerging in a regular sequence from the base, the laterals preceding the alternates by ca. 18 spirals; anthers pinkish to orange-purple, 0.3–0.5 mm long, 0.2–0.7 mm wide, inclined over and obscuring the pistil; thecae oblong-ellipsoid to obovoid, slightly or not divaricate; pollen yellow, fading to white, faintly yeasty-scented. *Infructescence* pendent; spathe deciduous or persisting; spadix 24–46 cm long, 1.5–2 cm diam.; berries purple-violet, oblong; mesocarp juicy; seeds white.

Anthurium loretense is currently known mainly from Peru in Loreto (hence the name) and Ucayali Departments at less than 350 m in a tropical moist forest life zone. A few collections are also known from Napo and from Morona–Santiago in Ecuador, Amazonas, Pasco, and San Martín in Peru, near Leticia in southernmost Colombia, and southwestern Amazonas in Brazil.

This species is characterized by its hook-shaped cataphylls, D-shaped petioles, large, broadly elliptic-oblanceolate blades drying greenish brown to brown, and by its long-pedunculate, mostly pendent inflorescence with the spathe usually ⅔ or up to ¾ as long as the long-tapered, maroon to purplish violet spadix and often held parallel to it. Although the base of the leaf blade is normally shallowly cordate with several congested primary lateral veins per side (appearing basal), leaf blades of younger plants are frequently acute to attenuate at the base.

Anthurium loretense is probably most closely related to (and perhaps only subspecifically distinct from) *A. cataniapoense* from southern Venezuela. That taxon shares many features, including similar petioles, cataphylls and inflorescences. *Anthurium cataniopoense* differs, however, in having a generally much smaller and more slender spadix and a more slender peduncle. *Anthurium loretense* is also similar to *A. harlingianum*, of Ecuador and Colombia, which differs in occurring at 450 to 1,800 m and in having a mostly erect inflorescence averaging about 6 cm shorter than that of *A. loretense*. See under *A. harlingianum* for details.

An interesting species also apparently closely related to *A. loretense* is *A. vaupesianum*, known only from Amazonian Colombia. It differs most markedly from *A. loretense* by its small size, more obovate leaf blades, and proportionally more slender spadix.

One collection from near Iquitos (*Croat 19342*) is noteworthy. Though closest to *A. loretense* among the species in the area, it appears closer still to *A. harlingianum* because of its erect inflorescence, moderately stubby spadix and leaves drying a very similar brown color. However, it differs from both of the above species in having the spathe longer than the spadix. It perhaps represents a new species; *Williams 2465* from near Leticia, Colombia, appears to represent the same taxon.

Two further collections from Loreto (*Vásquez et al. 4882* and *Rimachi 5569*) possibly belong here. The Vásquez collection has a leaf blade only 54–62 cm long and petioles 17–21 cm long, and the Rimachi collection has a spadix (at anthesis) reported as green. In addition, both collections have blades long-attenuate toward the base (ending abruptly acute at the base) and shortly stipitate spadices. Another collection (*Smith 2881*) from Oxapampa in Pasco Department, Peru, appears to belong here as well, although it is very far removed from the known range of *A. loretense*. *Gentry et al. 29912* (perhaps a mixed collection) from near Iquitos, has leaf blades that are very long-attenuate in the lower third and narrowly acute at the base. It otherwise appears to belong here.

Mention should be made of several collections from the rather isolated valley of the Río Santiago and the adjacent Río Cenepa valley in Amazonas Department, Peru, the only ones known from this department. These differ in having more flowers per spiral (10–18 vs. 5–13) and relatively shorter

peduncles (1.5–2 vs. 4–12(20)× longer than the petioles). Local names for these plants include "uyayugkunamu" and "kagkur nuka" (Huambisa tribe); "tukum" and "mun tukui" (Río Cenepa).

BRAZIL. AMAZONAS: Rio Jutai, 5°12′S, 69°00′W, *Traill 1138* (K). COLOMBIA. AMAZONAS: Quebrada Arara, 2 hr. N of Leticia near Río Amazonas, *Croat 7536* (MO, F). Puerto Nariño, Parque Nacional Amacayacu, 100 m, 3°45′S, 70°15′W, *Vásquez et al. 12504* (MO); Río Miritiparana, Caño Guacaya, 700 ft., 0°30′S, 70°40′W, *Schultes & Cabrera 16239* (GH). ECUADOR. MORONA-SANTIAGO: 35 km NE of Montalvo, 260 m, 1°49′S, 76°42′W, *Zak & Espinoza 4590, 4680* (MO). NAPO: Lago Agrio–Coca, ferry road 7.2 km S of Río Aguarico, 270 m, 0°02′N, 76°51′W, *Croat 58643* (MO, QCA); Lago Agrio–Río San Miguel, 5 km N of Lago Agrio, 280 m, 0°05′N, 76°55′W, *Croat 58689, 58691* (MO, QCA); 17.3 km N of Lago Agrio, *Croat 50344* (MO); Lago Agrio–Río San Miguel, 3 km from San Miguel, 350 m, *Besse et al. 1549* (SEL); Lago Agrio–Puerto El Carmen de Putomayo, vic. Tarapoa, 240 m, *Croat 58632A* (MO); Río Arajuno, Hacienda Aguinda, 450 m, 1°07′S, 77°36′W, *Marles EE 13* (MO). NAPO: Puerto Napo–Misahuallí, junction of Río Misahuallí and Río Napo, Vereda Venecia, 3.8 km W of Misahuallí, 370 m, 1°02′S, 77°42′W, *Croat 58895* (MO, QCA); Río Cuyabeno, 1.5 km upstream from Puerto Bolívar, 300 m, 0°06′S, 76°10′W, *Brandbyge et al. 33700* (AAU, MO); N of Laguna Grande, 265 m, *Poulsen 79710* (AAU); Parque Nacional Yasuní, 230 m, 0°52′S, 76°05′W, *Cerón 3354* (MEXU, MO, QCNE); 200 m, *Cerón & Gallo 4937* (MO, QCNE), *53396* (B, MO, QCNE); Añangu, in NW corner of park, 300 m, 76°22–23′W, 0°32′S, *Korning 47126* (AAU); Poso petrolero Daimi 2, 200 m, 0°55′S, 76°11′W, *Cerón & Hurtado 4096* (MO). PERU. AMAZONAS: Quebrada Chigkishinuk, *Kayap 282* (MO, US); Río Cenepa, Cenepa–Tuhushiku Creek, 700–800 ft., *Berlin 1874* (MO); Quebrada Huampami, vic. Kachaim, vic. Huampami, 5 km E of Chávez Valdivia, 200–250 m, 4°30′S, 78°30′W, *Kujikat 398* (MO); Río Santiago, Quebrada Caterpiza, 2–3 km behind community of Caterpiza, 65 km N of Pinglo, 200 m, *Huashikat 1343, 1869, 2343* (MO); 800 m below community of Caterpiza, trail from Mitayar, W side of Q. Caterpiza, 200 m, *Huashikat 487* (MO). LORETO: Quebrada Nawampa, 150 m, 4°30′S, 44°10′W, *Croat 17694* (MO); Quebrada Tahuayo, SSW of Tamshiyacu, *Croat 19743* (MO); Río Aguaytia, Aguaytia, 9°02′S, 75°30′W, *Croat 20947* (MO, USM); Río Nanay, Mishana, 120 m, *Solomon 3518* (MO); Prov. Alto Amazonas, Río Pastaza, Andoas, 210 m, 2°48′S, 76°28′W, *Gentry et al. 29672* (MO); Prov. Loreto, Río Tigre, Vista Alegre, 240 m, 2°40′S, 75°35′W, *Lewis et al. 12841* (MO); Prov. Maynas, Alpahuayo (Estación IIAP), *Vásquez et al. 5981* (MO); Iquitos Region, Río Itaya, Palo Seco, *Revilla et al. 2594* (F, MO); Iquitos–Nauta, 130 m, *Vásquez et al. 10696* (AMAZ, MO); Caserio de Nuevo Esperanza, 110 m, *Rimachi 5569* (IBE); Río Maniti, Recreo, NE of Iquitos, 115 m, 3°42′S, 72°50′W, *Vásquez & Jaramillo 1128* (MO); Río Momón, rear of Fundo Bohallo, 1 hr. upriver from mouth, 130 m, *Diaz & Jaramillo 78* (CM, K, M, MO); 1 km from the Río Nanay, Quebrada Mamoncillo, 220 m, 3°43′S, 73°20′W, *Croat 51225* (CAS, DUKE, K, MO, US, USM), *51226* (AAU, B, CM, K, MO, RSA, US, USM); below Balcon, ca. 95 m, *McDaniel & Rimachi 26283* (IBE); Río Amazonas, S of Iquitos, *Croat 19342* (MO, F); NE of Leticia (Colombia), Caballococha, 3°54′W, 70°32′W, *Williams 2465* (F); Quebrada de Sinchiqui below Santa María de Ojeal, *McDaniel & Rimachi 23873* (IBE); Dtto. Indiana, Explorama Inn, 220 m, 3° 23′S, 73°02′W, *Croat 61648* (AMAZ, MO); Río Amazonas, Quebrada del caserio de San Miguel, ca. 90 m, *Rimachi 5055* (IBE); Dtto. Yanamono, Indiana–mouth of Río Napo, Explorama Tourist Camp, 120 m, 3°28′S, 72°48′W, *Gentry et al. 29912* (CM, MO), *61651* (CM, MO), *Vásquez & Jaramillo 6321* (MO); 3°24′S, 72°49′N, 150–180 m, *Croat 61766, 61783* (AMAZ, MO), *Gentry et al. 36577* (MO); across Río Amazonas from Isla Yanamono, 150 m, *Croat 50126* (originally collected by Gentry, live at MO) (MO, U); Río Napo, Quebrada Sucusari, 130–140 m, 3°15′S, 72°55′W, *Gentry et al. 42695, 54535* (MO); Explor. Napo Camp, 130 m, 3°20′S, 72°55′W, *Vásquez & Jaramillo 11829* (MO, QCA), *11835* (MO); Quebrada Paparo, Río Manati, 110 m, 3°45′S, 72°55′W, *Vásquez & Jaramillo 11654* (MO); Explorama Llachapa Camp, Quebrada Sucusari, below Mazán, 140 m, *Gentry et al. 27737* (MO); Río Tamshiyacu, Caseria Alianza, 130 m, 4°05′S, 72°58′W, *Gentry et al. 29233* (BM, MO), *Vásquez & Jaramillo 4376* (MO); Puerto Alianza, 160 m, 4°08′S, 72°55′W, *Vásquez & Criollo 1836* (MO); Prov. Requena, Río Tapiche, Yarina, 180 m, 5°05′S, 73°50′W, *Vásquez et al. 4882* (MO); Jenaro Herrera, 140 m, *van der Werff et al. 10061* (MO). PASCO: Prov. Oxapampa, Iscozazin, 350 m, 10°11′S, 75°13′W, *Smith 2881* (MO). SAN MARTÍN: Tarapoto–Yurimaguas, km 55, NE of Pongo de Canarachi, 230 m, 6°15′S, 76°15′W, *Gentry et al. 52272* (MO).

Anthurium luteynii Croat, Selbyana 5(3–4): 324. 1981. TYPE: Panama. Veraguas: Río Primero Brazo, 2.5 km beyond Escuela Agrícola Alto Piedra, beyond Santa Fe, 700–750 m, *Croat 25521* (holotype, MO 2827506-08; isotypes, B, C, CAS, CM, CR, DUKE, F, K, M, MEXU, NY, PMA, SEL, UCLA, US, VEN). Figures 18, 187–189, 195.

Epiphytic or terrestrial; stem short; roots descending, whitish green, smooth to weakly pubescent, blunt at apex, 2–5 mm diam.; cataphylls subcoriaceous, elliptic, 10–28 cm long, minutely apiculate and inequilateral at apex, drying tan, persisting intact, soon dilacerating into reticulum of fibers. *Leaves* erect to spreading; petioles 9–50 cm long, 1.3–2.5 cm diam., ± trapezoidal to thicker than broad, flattened to weakly sulcate, sometimes with weak rib diminishing toward the base adaxially, the margins prominently and sharply raised, sharply and prominently 1–3-ribbed abaxially, the surface minutely pale-speckled; geniculum much thicker and paler than petiole, 1–3 cm long; blades thickly coriaceous, oblong-elliptic to oblong-oblanceolate, gradually to abruptly acuminate at apex (the acumen apiculate), acute to obtuse at base, 50–125 cm long, 9–33 cm wide, broadest near or above the middle; upper surface

weakly glossy to semiglossy, dark green, lower surface matte, paler; midrib flat at base, becoming convexly raised toward the apex, much paler than surface above, prominently higher than broad and sharply 1–3-ribbed at base below, gradually becoming prominently and obtusely to acutely angular and eventually convex toward the apex, paler than surface; primary lateral veins 10–25 per side, departing midrib at 60–70° angle, slightly arcuate-ascending, weakly raised in grooves above, narrowly and convexly raised below; interprimary veins sunken above, flat or slightly raised and darker than surface below; tertiary veins obscure above, darker than surface below; collective vein arising from near the base, sometimes in the upper third of the blade, sunken or ± obscure above, weakly raised to flat and darker than surface below, 3–10 mm from margin. *Inflorescences* erect-spreading and slightly arching, equaling or shorter than leaves; peduncle 49–85 cm long, 1.3–2 cm diam., 0.5–3(6.6)× as long as petiole, green to violet-purple, with prominent rounded rib adaxially, more prominently ribbed abaxially; spathe erect to cucullate, hooding the spadix, coriaceous, dark purple, narrowly ovate to oblong-lanceolate, 9–33.5 cm long, 2–11 cm wide, broadest in the lower third, inserted at 60° angle on peduncle, acuminate at apex (the acumen caudate, to 15 mm long), decurrent at base; spadix violet-purple to maroon, shortly tapered toward apex (occasionally toward both ends), 7–18 cm long, 8–28 mm diam. near base, 5–17 mm diam. near apex; flowers rhombic to slightly 4-lobed, 2–3.6 mm long, 1.8–3 mm wide, the sides straight to jaggedly sigmoid; ca. 15 flowers visible in either spiral; tepals matte to semiglossy, minutely punctate, covered with dust-like waxy bloom; lateral tepals 1.2–1.5 mm wide, the inner margins turned up against pistil; pistils exserted ca. 0.5 mm, green at base, purplish brown at apex; stigma 1 mm long, droplets copious, appearing 3–4 weeks before stamens emerge; stamens emerging in a scattered pattern throughout spadix, lateral stamens emerging to apex before alternates start emerging; anthers creamy, 0.4–0.5 mm long, 0.6–1 mm wide; thecae ellipsoid, slightly divaricate; pollen yellow-orange fading to white. *Infructescence* erect or spreading; spathe cucullate and withered; spadix 20–25 cm long, to 4 cm diam.; berries orange to yellow (B & K yellow 8/25), oblong-ellipsoid to obovoid, acute at apex, 8.9–19 mm long, 5–8 mm diam.; pericarp thickened, transparent in lower half with few raphide cells; mesocarp mealy, orange; seeds 2 per berry, tan, oblong, 4–6.5 mm long, 2–2.7 mm diam., ca. 2 mm thick, weakly beaked at both ends.

Anthurium luteynii is known only from Panama, on both slopes of the Continental Divide, in tropical wet and premontane rainforest life zones at elevations of 530 to 1,350 m.

This species is characterized by its coriaceous, more or less narrowly oblanceolate leaves and its somewhat trapezoidal petiole that is prominently three-ribbed abaxially and sharply sulcate adaxially. Also characteristic is the stout, semi-erect inflorescence with a broad, often cucullate, purplish spathe and violet-purple spadix and the long, sharply pointed, orange berries.

Although initially confused with *Anthurium seibertii* because of its orange, pointed berries and coriaceous, persistent, intact cataphylls, *A. luteynii* is not believed to be closely related to that species or to any other known species. *Anthurium seibertii* differs from *A. luteynii* principally in having thinner, strap-shaped leaves with the collective vein always arising from near the base, and in having a narrowly tapered, much paler violet-purple spadix.

PANAMA. BOCAS DEL TORO: Fortuna Road, Gualaca–Chiriquí Grande, 33 km from Gualaca, 530 m, 8°36′N, 82°19′W, *Hoover 1334* (MO). COCLÉ: N of El Valle de Antón, trail to Las Minas, 800–900 m, *Luteyn 3162* (DUKE, MO); El Copé Region, sawmill 7 km NE of El Copé, 600 m, *Antonio 1140* (MO); Alto Calvario above El Cope, 8°39′N, 80°36′W, *Croat 68773* (MO); El Valle Region, Cerro Gaital, N slopes of mountain near La Mesa, N of El Valle, 800–900 m, 8°40′N, 80°7′W, *Knapp & Dressler 4881* (MO); El Valle de Antón, La Mesa, *Folsom 2785* (MO); El Valle de Antón, 2 km W of Cerro Pilón, La Mesa, 860–900 m, *Croat 37416* (MO); beyond La Mesa, toward Los Llanos, *Luteyn 3163* (DUKE). DARIÉN: Río Tuquesa headwaters, 2 km by air from Continental Divide, upper gold mining camp of Tyler Kittredge, 700 m, *Croat 27120, 27156, 27169* (MO). PANAMÁ: Cerro Jefe, ridge above Altos de Azul to Río Chagres, 9°15′N, 79°30′W, *McPherson 11900* (MO). VERAGUAS: Santa Fe Region, vic. Escuela Agrícola Alto Piedra, 735–770 m, *Croat & Folsom 33993* (MO), *Hammel 4669* (MO), *Mori & Kallunki 4751* (MO); Río Santa María, road from Santa Fe, *Witherspoon & Dressler 8923* (MO); Cerro Tute, 830–1,150 m, *Croat 48909* (MO); *D'Arcy 14982* (MO); Río Primero Brazo, 2.5 km beyond school 700–750 m, *Croat 25521* (B, C, CAS, CM, CR, DUKE, F, K, M, MEXU, MO, NY, PMA, SAR, SEL, UCLA, US, VEN), *48990* (MO), *49071* (FTG, MO); NW of Santa Fe, W fork of road beyond school, 1,300 m, *Croat 49044* (CM, ENCB, IBE, K, MO, VDB).

Anthurium machetioides Matuda, Anales Inst. Biol. Univ. Nac. Mexico 22: 379, fig. 7. 1952. TYPE: Mexico. Oaxaca: Chinantia, 1,200 m, *Ramírez 144* (holotype, MEXU). Figure 190.

Description based on dried material only. Stem short; cataphylls thin, to 6.5 cm long, drying brown,

persisting as linear fibers, probably deciduous. *Leaves* with petioles 6–7 cm long, 4–5 mm diam., broadly sulcate adaxially, rounded abaxially; geniculum 0.4–0.5 cm long; blades, oblanceolate, narrowly acuminate at apex, narrowly cuneate at base, 45–48 cm long, 6–8 cm wide, broadest above the middle, both surfaces matte; midrib prominently and narrowly raised above and below; primary lateral veins 10–15 per side, departing midrib at 20–30° angle, arcuate to the collective vein; reticulate veins prominulous; collective vein arising from one of the lowermost primary lateral veins, 3–4 mm from margin. *Inflorescences* equaling or longer than leaves; peduncle 40–48 cm long, to 5 mm diam., terete; spathe narrowly lanceolate, inserted at 45° angle on peduncle; spadix greenish, glaucous, long-tapered, 20–24 cm long, 13 mm diam. near base, 6 mm diam. near apex; flowers rhombic, 2–2.4 mm long, 2.4–2.6 mm wide; 13–14 flowers visible in principal spiral, 9–10 in alternate spiral; pistils not emergent; stigma ellipsoid, slitlike, 0.5 mm long; stamens emergent, held at edge of tepals; thecae ovoid.

Anthurium machetioides is endemic to central Mexico on the Atlantic slope. The type was from the region of Chinantla in northeastern Oaxaca (a region comprising parts of four districts south of Valle Nacional), at 1,200 m in "selva baja caducifolia," and a second collection was made relatively nearby at 200 m in the District of Tuxtepec (between Valle Nacional and Tuxtepec).

This species is characterized by its oblong-linear leaves with a collective vein arising from near the base, primary lateral veins that are scarcely more prominent than the tertiary veins, and a very elongate, gradually tapered spadix.

In describing this species Matuda posited its relationship as sect. *Leptanthurium*; however, despite the fact that it has a collective vein arising from the base, its affinities are more likely with *Anthurium schlechtendalii*, which often has a collective vein from near the base in juvenile leaves. It differs from *A. schlechtendalii* in its proportionally narrow leaves, the presence of a collective vein, and in its proportionally much longer spadix.

MEXICO. OAXACA: Chinantla, 1,200 m, *Ramírez 144* (MEXU); Dist. Tuxtepec, Chiltepec, 200 m, *Martínez-Calderón 844* (LL, MICH).

Anthurium maguirei A. Hawkes, Bull. Torrey Bot. Club 75: 633. 1948. TYPE: Surinam. Table Mountain, 564 m, *Maguire 24218* (holotype, NY; isotypes, F, US). Figure 191A.

Description based on dried material only. Terrestrial or epiphytic; stem moderately elongate, horizontally creeping; internodes short, 0.8–1 cm diam.; roots moderately few, brownish, smooth, moderately slender and elongate, ca. 2–3 mm diam.; cataphylls broadly triangular, 1.5–3.5 cm long, acute at apex, reddish brown to dark brown, persisting intact. *Leaves* with petioles 4.5–21 cm long, ca. 2–3 mm diam., apparently subterete or C-shaped, sharply and narrowly sulcate adaxially, rounded abaxially; geniculum slightly thicker than petiole, 0.3–0.7 cm long; blades coriaceous, oblong-ovate to broadly elliptic, obtuse at apex (the acumen apiculate), rounded (occasionally obtuse) at base, 9.5–16 cm long, 2.8–5.7 cm wide, broadest at or below the middle; both surfaces matte, yellowish brown; midrib apparently acutely raised above, convexly raised below; primary lateral veins 5–8 per side, departing midrib at 30–45° angle, arcuate, probably flat or weakly sunken above, raised below; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins weakly raised below; collective vein arising from near the apex, sunken above, raised below, equally as prominent as primary lateral veins, 2–6 mm from margin. *Inflorescences* longer than leaves; peduncle 22–26.5 cm long, ca. 2–3 mm diam., 3.1–5.5× as long as petiole, terete; spathe probably spreading or reflexed, subcoriaceous, green, lanceolate, 3–4 cm long, 0.6–0.8 cm wide, broadest near the base, acuminate at apex (the acumen inrolled, 1–2 mm long), acute at base; stipe 2–2.2 cm long in front, 1.7–1.8 cm long in back; spadix green, cylindroid, 4.3–4.5 cm long, 4 mm diam.; flowers square, 2–2.4 mm in both directions, the sides straight to smoothly sigmoid; 5–6 flowers visible in principal spiral, 3–4 in alternate spiral; tepals apparently smooth; lateral tepals 1.2–1.5 mm wide, the inner margins straight, the outer margins 2-sided; pistils exposed; stigma linear, 0.2–0.3 mm long; anthers 0.4 mm long, 0.5 mm wide, inclined over and obscuring the pistil; thecae oblong-ovoid, slightly divaricate. *Infructescence* not seen.

Anthurium maguirei appears to be a local relict of the Guiana Shield flora, known only from Table Mountain in Surinam at 564 to ca. 1,000 m. It has been recorded as growing terrestrially in a "marshy" area as well as "terrestrial/epiphytic, climbing," although the last attribution is dubious.

This species is characterized by its very small size, moderately elongate stem and more or less elliptic leaf blades. It is one of the most distinctive species within sect. *Pachyneurium* and is unlikely

to be confused with any other. Its presumed closest ally is *A. bonplandii* subsp. *bonplandii*, which is much larger in overall size and occurs further to the west at lower elevations.

Anthurium yutajense is another relict species of the Guiana Shield which superficially resembles *A. maguirei*. The former is placed provisionally in sect. *Urospadix* because its leaf blades have a collective vein originating at the base, while leaves of *A. maguirei* have free-ending (except near the apex) primary lateral veins.

SURINAM. Table Mountain, 564 m, *Maguire 24218* (F, NY, US); Tafelberg, *Herbarium Suriname Forest Service 16571* (MO, U).

Anthurium manabianum Croat, sp. nov. TYPE: Ecuador. Manabí: Portoviejo–Pichincha, 12 km E of San Plácido, 450 m, *Harling & Andersson 24750* (holotype, GB 1304-9, 1304-10). Figures 191, 192.

Planta terrestris aut epiphytica; petiolus 22 cm longus, 6–8 mm diam., complanatus; lamina late oblanceolata, 95.5 cm long, 27 cm lata; pedunculus 24 cm longus; stipes 2.5–3 cm longus; spadix cylindricus, 6.5–10 cm longus, 4 mm diam., purpureo-brunneus.

Description based on dried material only. Terrestrial; stem, roots and cataphylls unknown. *Leaves* spreading; petioles 22 cm long, 6–8 mm diam., apparently flattened adaxially, with sharply raised margins; geniculum slightly darker and scarcely thicker than petiole, 1 cm long; sheath 3 cm long; blades chartaceous (probably young), broadly oblanceolate, shortly acuminate at apex, long-attenuate at base, 95.5 cm long, 27 cm wide, broadest in the upper third, the margins slightly sinuate; both surfaces nearly matte, gray-green; midrib weakly and convexly raised toward the base, more prominently raised toward the apex above, prominently convex below; primary lateral veins ca. 27 per side, departing midrib at 40–50° angle, straight to the collective vein, convexly raised above, less conspicuously so below; interprimary veins absent except near the apex, almost as conspicuous as primary lateral veins; tertiary veins obscure above, weakly visible below; reticulate veins not visible; collective vein arising from near the base, as conspicuous as larger tertiary veins, 2–8 mm from margin. *Inflorescences* spreading; peduncle 24 cm long, 2 mm diam., 1.1× as long as petiole, green, terete; spathe erect-ascending, chartaceous, green with numerous, conspicuous raphide cells, oblong-elliptic, 9–10 cm long, 1.3–1.5 cm wide, broadest at or near the middle, acuminate-caudate at apex (the acumen 10 mm long), obtuse-rounded at base; stipe 2.5–3 cm long; spadix purplish brown, cylindroid, moderately curved, semi-erect, held at ca. 30–40° angle from peduncle, 6.5–10 cm long, 4 mm diam. throughout or 3 mm diam. near apex; flowers square, 1.2–2 mm long, 1.5–2 mm wide, the sides straight to smoothly or jaggedly sigmoid; 3–5 flowers visible in principal spiral, 5–8 in alternate spiral; tepals very weakly papillate; lateral tepals 0.9–1.1 mm wide, the inner margins rounded, weakly erose, the outer margins 3-sided; pistils not visible; stamens ± erect; filaments exserted 0.2–0.4 mm; anthers brownish yellow, 0.5–0.6 mm long, 0.2–0.4 mm wide; thecae oblong-ellipsoid, not divaricate. *Infructescence* not seen.

Anthurium manabianum is known only from the type specimen, collected in Ecuador in Manabí Province (hence the name) in a premontane wet forest life zone at 450 m.

This species is characterized by its broadly oblanceolate, thin, greenish drying blades which are shortly acuminate at the apex and attenuate at the base, and by its small, long-stipitate, weakly tapered, purplish brown spadix.

Anthurium manabianum appears to be superficially similar to *A. lennartii*; see discussion of that species for details.

ECUADOR. MANABÍ: Portoviejo–Pichincha, 12 km E of San Plácido, 450 m, *Harling & Andersson 24750* (GB).

Anthurium manuanum Croat, sp. nov. TYPE: Peru. Madre de Dios: Manú, Salvación a Gloria, 710 m, *Vargas 17747* (holotype, CUZ). Figure 192A.

Planta epiphytica; internodia ad 1.5 cm diam.; cataphyllum persistens intactum apud nodos superiores; petiolus 4.5–9 cm longus, 3–4 mm diam., D-formatus, adaxile sulcatus, margine et costa media manifeste elevata; lamina subcoriacea, oblanceolata, 26–39 cm longa, 7–12 cm lata. Inflorescentia tam longa quam petioli; pedunculus 8 cm longus; spatha linearis-lanceolata, 4–5 cm longa, 8 mm lata; spadix glaucus, cylindricus, 4.2 cm longus, 3–4 mm diam. Baccae ignotae.

Description based on dried material only. Epiphytic; stem 1.5 cm diam.; roots brownish gray, densely woolly-pubescent, elongate, at least 3 cm long, 1–1.5 mm diam.; cataphylls probably subcoriaceous, 3–7.5 cm long, acuminate at apex, brown to brownish gray, persisting intact at least at the upper nodes, probably persisting as a reticulum of fibers on the lower ones. *Leaves* erect to spreading; petioles 4.5–9 cm long, 3–4 mm diam., ± D-shaped, sulcate with the margins and medial rib prominently raised adaxially, ± rounded abaxially; geniculum slightly darker than petiole, ca.

0.5–0.9 cm long; sheath 1.5–2.3 cm long; blades subcoriaceous, oblanceolate, acuminate at apex (the acumen ca. 2 cm long, apiculate), long-attenuate at base, 26–39 cm long, 7–12 cm wide, broadest above the middle, the margins probably undulate; upper surface matte, lower surface matte to semiglossy, both surfaces tan to dark brown; midrib prominently convex at base, becoming sharply acute toward the apex above, convexly raised and slightly darker than surface below; primary lateral veins 6–7 per side, departing midrib at 50–55° angle, straight, becoming arcuate-ascending to the margin or to the collective vein in the upper third of the blade, prominently raised above, flat to weakly raised below, slightly paler than surface; interprimary veins few, weakly raised above and below; tertiary veins prominulous, very weakly raised above and below; collective vein arising from near the apex, very weakly raised above and below, 4–7 mm from margin. *Inflorescences* erect, much shorter than leaves; peduncle 8 cm long, 1–2 mm diam., about equalling petiole, dark brown; spathe reflexed, subcoriaceous, brownish, linear-lanceolate, 4–5 cm long, 0.8 cm wide, broadest near the base, acuminate at apex, acute at base; stipe ca. (2)7 mm long in front, 1–2 mm long in back; spadix grayish brown, glaucous, cylindroid, held at 150° angle from peduncle, 4.2 cm long, 3–4 mm diam.; flowers rhombic, 1.9–2.3 mm long, 1.5–1.8 mm wide, the sides jaggedly sigmoid, sometimes straight; 6–7 flowers visible in principal spiral, 4–6 in alternate spiral; tepals densely papillate; lateral tepals 1.2–1.4 mm wide, the inner margins straight, occasionally broadly convex, pale, erose, the outer margins 2–3-sided, a few 4-sided; pistils with exposed area 0.6–1 mm diam., ± square; stigma ± ellipsoid; anthers yellowish, ca. 0.6 mm wide. *Infructescence* not seen.

Anthurium manuanum is known only from Peru in the Department of Madre de Dios, in the Manú region (hence the name), at 260 to 840 m. It probably occurs in a subtropical moist forest life zone.

This species is distinguished by its short peduncle (about as long as the petioles), green, oblong-lanceolate spathe and short, oblong, glaucous spadix, with the tepals having more or less erose margins.

Anthurium manuanum is most likely to be confused with, and is perhaps most closely related to, *A. uleanum*, which occurs further to the north. *Anthurium uleanum* differs in having much longer petioles and peduncles and a longer, more slender spadix. *Anthurium manuanum* may also be confused with *A. ernestii*, but differs mainly in having a conspicuously glaucous spadix.

PERU. MADRE DE DIOS: Manú, Salvación a Gloria, 710 m, *Vergas 17747* (CUZ); Prov. Manú, Cerro de Pantiacolla, Río Palotoa, 10–15 km NNW of Shintuya, 840 m, 12°35′S, 71°18′W, *Wachter 54* (F); Manú National Park, Cocha Cashu uplands, 400 m, 11°45′S, 71°0′W, *Nuñez 5769* (MO); Tambopata, Comunidad Nativo de Infierno, Hermosa Chica, 260 m, 12°49′S, 69°20′W, *Alexiades & Pesha 972* (NY).

Anthurium martianum K. Koch & Kolb in K. Koch, Wochenschr. 11: 276. 1868. TYPE: Surinam? Cultivated. Engler's Araceae Exsiccatae #165 (lectotype, B; isolectotypes, GH, P). Figures 194, 194A, 196.

Habit unknown; stem short; internodes to 2.5 cm diam.; roots spreading, rather short, tapered; cataphylls coriaceous, oblong-lanceolate, to 12 cm long, acuminate at apex, drying tan, persisting semi-intact. *Leaves* erect-spreading; petioles (11)20–37 cm long, 5–12 mm diam., obtusely and narrowly sulcate adaxially, rounded abaxially; geniculum thicker than petiole, 3–4 cm long; blades (dried) subcoriaceous, oblong-elliptic to oblong-lanceolate, acuminate at apex (the acumen thick and inrolled), rounded to truncate (34)43–103 cm long, (6)20–38 cm wide, broadest slightly below or at the middle, the margins weakly undulate; upper surface semiglossy, dark green, paler below, both surfaces drying greenish gray to brownish; midrib raised above, slightly paler than surface, convexly raised below; primary lateral veins 18–24 per side, departing midrib at 55–85° angle, weakly curved to the collective vein, raised above and below; interprimary veins less conspicuously raised than the primary lateral veins; tertiary veins weakly raised above and below; collective vein arising from near the base, weakly raised above and below, 5–35 mm from margin. *Inflorescences* (dried) with peduncle 25–60 cm long, 4–7 mm diam., ca. 0.7–1× as long as petiole, terete; spathe spreading to reflexed, subcoriaceous to coriaceous, green, lanceolate, 9.5–17 cm long, 1.5–4 cm wide, broadest near the base, inserted at 60° angle on peduncle, acuminate at apex (the acumen tightly inrolled, ca. 6 mm long), rounded at base; spadix maroon, subsessile, tapered, weakly curved, held at 150–165(185)° angle from peduncle, 9–15 cm long, 7–11 mm diam. near base, 3–4 mm diam. near apex; flowers rhombic, 1.9–2.6 mm long, 1.6–2.1 mm wide, the sides mostly straight to smoothly or jaggedly sigmoid; 11–12 flowers visible in principal spiral, 12–18 in alternate spiral; tepals minutely

and densely papillate when dried; lateral tepals 1.1–1.5 mm wide, the inner margins convex, weakly erose, the outer margins 2–3-sided; pistils ca. 0.8 mm long, 0.5 mm wide; stigma oblong, 0.4–0.6 mm long; thecae oblong, slightly or not divaricate; pollen fading to cream-white. *Infructescence* not seen.

Anthurium martianum is known from a single live collection, purportedly from Surinam, that was propagated at the botanical gardens in Berlin, Kiel, and Munich. The herbarium material is highly uniform and appears to be the result of a single introduction. Because it is known only from cultivation and no field-collected herbarium vouchers exist, there is the possibility that it is a cultivated plant of hybrid origin. However, because the taxon is clearly distinct, it will be retained here.

This species is distinguished by its persistent spathe, short, yet very tapered spadix, moderately long petioles and its leaf blades, rounded at the base, with several pairs of congested lateral veins near the base, and with a collective vein arising from near the base.

Anthurium martianum is closest in appearance to *A. dombeyanum*, which has generally shorter petioles and more undulate leaf blades that are broadest above the middle.

A living collection at the Munich Botanical Garden (without number) labeled *A. martianum* and vouchered as *Croat 61178* perhaps represents this species; however, although it closely matches the plate in Gartenflora 20: t. 681 (1871), it is smaller and the primary lateral veins are fewer and not nearly as distinct as the type material.

SURINAM?. Cultivated. Engler's Araceae Exsiccatae #165 (B, GH, P). Cultivated at Munich, *Croat 61178* (MO).

Anthurium napaeum Engl., Bot. Jahrb. Syst. 25: 407. 1898. TYPE: Ecuador. Pichincha: Río Napac ("Napa"), *Sodiro s.n.* (holotype, B). Figures 197, 199, 200.

Anthurium peripense Engl., Bot. Jahrb. Syst. 25: 442. 1898. TYPE: Ecuador. Manabí: Río Peripa, *Sodiro s.n.* (holotype, B).

Anthurium rircayanum Sodiro, Anal. Univ. Centr. (Quito) 22(156): 21. 1906. TYPE: Ecuador. Guayas: Río Rircay, *Rimbach s.n.* (holotype, B).

Terrestrial, or caespitose on rocks, sometimes epiphytic; stems 9–30 cm long, 1.5–2.5 cm diam.; roots numerous, dense, spreading to descending, white to green, whitish or brown on drying, ± smooth, thick and short to slender and elongate, weakly tapered at apex, 2–4 mm diam.; cataphylls subcoriaceous, 8–9(16) cm long, acuminate and apiculate at apex, pale green, drying tan, persisting intact, eventually as a reticulum of fibers. *Leaves* erect to erect-spreading; petioles (8)16–42 cm long, 5–15 mm diam., broadly triangular, convex adaxially with weak medial ridge, the margins prominently and sharply raised, almost winged, bluntly to sharply angular abaxially, the surface conspicuously pale short-lineate; geniculum slightly thicker and paler than petiole, 1–2 cm long; blades moderately coriaceous, broadly lanceolate to oblong-elliptic to oblanceolate, long-acuminate at apex (the acumen short-apiculate), acute to obtuse at base, (31)40–70(82) cm long, (5)9–28 cm wide, broadest at or above the middle, the margins flat to broadly undulate; upper surface glossy, dark green, lower surface glossy to semiglossy, conspicuously paler; both surfaces matte when dried, green to brown; midrib prominently convex at base, becoming higher than broad toward the apex above, pale short-lineate and paler than surface, prominently and sharply acute-raised below, raised above and below when dried, paler than surface below, same as surface above; primary lateral veins numerous, ca. 20–30 per side, departing midrib at 50–75° angle, straight-ascending, weakly visible above and below when fresh, slightly raised on both surfaces when dried; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins weakly visible when dried; collective vein arising from near the base or in the upper third of the blade, slightly more prominent than primary lateral veins when fresh below, equally as prominent as primary lateral veins when dried, 2–13 mm from margin. *Inflorescences* erect to spreading, shorter than leaves; peduncle 23–50(62) cm long, 3–7 mm diam., sharply 2–3-ridged, 2–3× as long as petiole, green heavily tinged with red-violet at base, faintly red-violet toward the apex; spathe reflexed-spreading, subcoriaceous, green tinged with red-violet (B & K yellow-green 6/7.5), linear-lanceolate to lanceolate, 6–10 cm long, 0.4–1.5 cm wide, broadest near the base or in lower third, inserted at 60–70° angle on peduncle, long-acuminate at apex (the acumen inrolled), acute at base, the margins meeting at 90° angle; spadix brownish purple (B & K red-purple 2/10) to dark purple, rarely dark olive-green, cylindroid to weakly tapered, sessile or stipitate 1–2 mm, erect, 5.5–16 cm long, 5–6 mm diam. midway; flowers ± square to 4-lobed, 1.9–2.5 mm long, 2–2.4 mm wide, the sides jaggedly sigmoid; 4–6 flowers visible in principal spiral, 8–10 in alternate spiral; tepals matte to semiglossy, densely papillate; lateral tepals 0.7–1.2 mm wide, the inner margins straight, the outer margins

2-sided, sometimes weakly 4-sided; pistils raised but not emergent, or held slightly above the tepals, green; stigma ellipsoid, 0.4 mm long, brushlike; stamens emerging shortly above the tepals, laterals emerging almost to the apex before alternates emerge; filaments fleshy, translucent or purplish, 0.5–0.8 mm long, 0.4–0.8 mm wide; anthers yellow to purplish, 0.3–0.6 mm long, 0.4–0.7 mm wide, inclined over the pistil; thecae oblong, drying ovoid, scarcely divaricate; pollen white to yellow-orange fading to tan. *Infructescence* with spathe persisting; spadix 8–22 cm long, 0.5–1.4 cm diam.; berries reddish to dark purplish violet, ovoid, exserted, acute at apex, drying 4.2–6 mm long, 2–2.5 mm diam.

A member of series *Multinervia*, *Anthurium napaeum* occurs in Ecuador on the western slopes of the Andes, at 200 to 1,400 (1,800) m in premontane wet and premontane moist forest, and in Nariño, Colombia. One specimen from Cotopaxi, between Latacunga and Quevedo at 800 to 950 m, was reported to occur in montane moist forest.

This species is characterized by its generally terrestrial habit, short, densely rooted stem, cataphylls that persist as a reticulum of fibers, broadly triangular, conspicuously pale-speckled petioles, leaf blades which are usually glossy on both surfaces when fresh, drying green and often conspicuously paler below, and by its cylindroid, brownish purple spadix with 4–6 flowers visible in the principal spiral.

Anthurium napaeum is most closely allied to *A. palenquense*, which differs in having leaf blades with the margins conspicuously concave toward the base.

The names *Anthurium peripense* and *A. rircayanum* are synonymized here for the first time. The type localities of these species, together with that of *A. napaeum* are in the coastal lowlands of western Ecuador, draining into the Gulf of Guayaquil. The differences between the type specimens are slight, the main one being leaf shape: the types of *A. napaeum* and of *A. rircayanum* closely resemble each other in this respect, while that of *A. peripense* has straighter blade margins which are somewhat concave toward the base.

An unusual collection (*Croat 55782*) exhibits stamens starting emergence at the apex of the spadix and progressing regularly to the base, with the laterals preceding the alternates by up to 18 spirals. Basipetal maturation of the stamens has not been observed in any other *Anthurium*.

COLOMBIA. NARIÑO: La Planada, Salazar Finca 7 km above Ricaurte, 1,750 m, 1°08′N, 77°58′W, *Gentry et al. 35197* (COL, MO). ECUADOR. CAÑAR: Azoques–El Triunfo, 1 km S of La Delicia, 2°27′S, 79°10′W, *Croat 50876* (AAU, B, CAS, K, CM, M, MO, RSA, US); Azogues–El Triunfo, 5 km W of La Delicia, 8 km SE of El Truncal, 600 m, 2°27′S, 79°15′W, *Croat 50904* (CM, MO). CARCHI: Peñas Blancas, 900 m, *Christenson 1535* (MO). CHIMBORAZO: Sibambe, 1,000–1,600 m, *Solís 5342* (F); Río Chanchán, 5 km N of Huigra, 1,667–2,167 m, *Camp 3428* (NY). COTOPAXI: Quevedo–Latacunga, 800–950 m, 0°55′S, 79°10′W, *Holm-Nielsen et al. 3021* (AAU); Río Pilaló, Quevado–Latacunga, Tenefuerste, 750–1,300 m, *Dodson & Gentry 11987, 12297, 12797* (MO, SEL); 3 km E of El Palmar, 800 m, *Dodson & Gentry 10267* (MO, SEL); 55.5 km from Quevedo, 23.5 km E of La Maná, 930–950 m, 0°53′S, 79°04′W, *Croat 57035* (CAS, BG, K, MBM, MEXU, MO, P, PMA); Quevedo–El Corazón, 1.9 km NW of El Corazón, 67.5 km SE of Quevedo, 1,225 m, 1°07′S, 79°06′W, *Croat 55829* (MO, QCA); Río Angamarca, Quevedo–El Corazón, Las Juntas, 200 m, *Harling & Anderson 19025* (MO, GB); Quevedo–El Corazón, 63.4 km SE of Quevedo, 6 Km NW of El Corazón, slopes near waterfall above river, 1,030 m, 1°7′S, 79°7′W, *Croat 55782* (AAU, F, M, MO, NY, QCA, RSA, US). ESMERALDAS: 300 m, *Cobb 77* (MO). GUAYAS: Naranjal, Entable, below 500 m, *Lehmann s.n.* (K); Río Rircay, *Rimbach s.n.* (B). Junction of Provinces GUAYAS, CAÑAR, CHIMBORAZO & BOLÍVAR: Bucay, 420 m, *Camp 3648* (NY, MO). MANABÍ: Río Peripa, *Sodiro s.n.* (B). PICHINCHA: Quito-Santo Domingo de Los Colorados, Chiriboga Road, Estación Los Faisanes, 12 km from Río Pilatón, 1,400 m, *Harling & Andersson 23128* (GB); Río Pilatón, Alluruquín, 22 km E of Santo Domingo, 950 m, 0°15′S, 78°58′W, *Hammel & Wilder 16073* (B, K, MO); Km 23 on Santa Domingo-Puerto Limón road, 100 m, 0°21′S, 79°22′W, *Kvist 40676* (AAU); San Juan, La Palma, 930 m, *Croat 38739* (F, MO); Alluruquín-Chiriboga, 1,100 m, *Madison 4069* (K, SEL); Río Blanco, below confluence with Río Toachi, 300 m, *Harling 4516* (S); Río Napa, *Sodiro s.n.* (B).

Anthurium narinoense Croat, sp. nov. TYPE: Colombia. Nariño: Junín-Barbacoas road, 2–10 km N of Junín, 900–1,000 m, 1°30′N, 78°10′W, *Gentry et al. 55343* (holotype, MO 3486084; isotype, PSO). Figure 201.

Planta epiphytica; petiolus 12 cm longus, 7 mm diam., D-formatus; lamina oblongo-oblanceolata, basi attenuata, ad 93 cm longa, 16 cm lata; pedunculus ad 40 cm longus; spatha oblongo-lanceolata, ad 11 cm longa, 1.5 cm lata; spadix atrorubens, 17 cm longus, 5–6 mm diam.; baccae ignotae.

Description based on dried material only. Epiphytic; stem and cataphylls unknown. *Leaves* erect-spreading; petioles ca. 12 cm long, 7 mm diam., D-shaped, slightly convex adaxially, apparently rounded abaxially; geniculum 1.5 cm long; blades subcoriaceous, oblong-oblanceolate, acuminate at apex, long-attenuate at base, 93 cm long, 16 cm wide, broadest above middle, yellowish, the margins flat; midrib convexly raised above, prominently convexly raised below; primary lateral veins ca. 30

per side, departing midrib at 60–70° angle, slightly arcuate to the collective vein, slightly raised above and below; interprimary veins numerous, almost as conspicuous as primary lateral veins; tertiary veins scarcely raised above and below, more prominent below; collective vein arising from near the base, nearly as conspicuous as primary lateral veins, 5–9 mm from margin. *Inflorescences* erect-spreading; peduncle 40 cm long, ca. 5 mm diam., ca. 4× as long as petioles, terete; spathe reflexed, subcoriaceous, green, oblong-lanceolate, at least 11 cm long, 1.5 cm wide, broadest near base, inserted at 45° angle on peduncle, apex not seen, the base acute; spadix dark reddish, slightly tapered, ± straight, 17 cm long, 4 mm diam. near base, 3 mm diam. near apex; flowers rhombic, 2.4–2.8 mm long, 1.6–2 mm wide, the sides smoothly sigmoid; 7–8 flowers visible in principal spiral, 5–6 in alternate spiral; tepals ± smooth; lateral tepals ca. 1 mm wide, the inner margins straight, the outer margins 2–4-sided; anthers 0.2 mm long, 0.3 mm wide; thecae slightly divaricate. *Infructescence* not seen.

A member of series *Multinervia*, *A. narinoense* is known only from the type collection made in Nariño (hence the name), Colombia, at 900 to 1,000 m in pluvial forest.

Anthurium narinoense is distinguished by its large leaves (for the series), which dry yellow-green, and its slender, tapered spadix. It is apparently not closely related to any other species, but somewhat resembles *A. fasciale* and *A. santiagoense* from the eastern slopes of the Andes in Ecuador, which both have a more stubby spadix with more flowers in the principal spiral.

Anthurium narinoense is unusual in being the only species of *Pachyneurium* known from pluvial forest.

COLOMBIA. NARIÑO: Junín-Barbacoas, 2–10 km N of Junín, 900–1,000 m, 1°30′N, 78°10′W, *Gentry et al. 55343* (MO, PSO).

Anthurium nervatum Croat, Monogr. Syst. Bot. Missouri Bot. Gard. 14: 141. 1986. TYPE: Panama. Veraguas: valley of Río Tercero Brazo, beyond Escuela Agrícola Alto Piedra, above Santa Fe, 500–700 m, *Croat 27329* (holotype, MO 2253314; isotypes, F, K, PMA, US). Figures 198, 202.

Epiphytic, occasionally terrestrial; stem 10–75 cm long, 2.5–6 cm diam.; leaf scars 1–1.5 cm high, 2–3.5 cm wide; roots few, descending, greenish, pubescent, moderately thick and short, slightly tapered, 3–7 mm diam.; cataphylls subcoriaceous, lanceolate, 16–35 cm long, rounded to emarginate at apex with subapical apiculum ca. 5 mm long, green, drying tan (B & K yellow-red 9/10), persisting semi-intact, eventually as a reticulum of fibers. *Leaves* erect to spreading; petioles 18–100 cm long, 7–14 mm diam., bluntly to sharply quadrangular to D-shaped or subterete, prominently to weakly sulcate or flattened adaxially, the margins flat or raised, rounded abaxially, the surface pale-speckled; geniculum thicker and paler than petiole, becoming fissured transversely with age, 1.5–5 cm long; blades moderately to thickly coriaceous, triangular to ovate-triangular, ovate-elliptic, acute to acuminate at apex (the acumen weakly apiculate), subcordate to cordate at base, sometimes decurrent on petiole, 27–98 cm long, 14.5–46 cm wide, broadest in the lower fourth of the blade, the margins broadly undulate; anterior lobe 25.5–90 cm long, the posterior lobes 4–19 cm long, directed downward and sometimes inward or outward; sinus arcuate with blade decurrent on petiole, to spathulate; upper surface matte to semiglossy, dark green, lower surface semiglossy, slightly paler; midrib bluntly angular-raised, becoming acutely to obtusely raised, and then weakly sunken at apex above, prominently and convexly raised below, paler than surface above and below; basal veins 3–6 pairs, often free to base, 2nd and 5th sometimes coalesced 1.5–2 cm, convexly raised above and below (less so below); primary lateral veins 19–25 per side, departing midrib at 50–60° angle, straight or weakly arcuate to the collective vein, prominently to weakly convexly raised above (more so below), paler than surface; interprimary veins sometimes present; tertiary veins obscure to weakly visible above, flat and darker than surface below; collective vein arising from one of the lowermost primary lateral veins or 1st to 2nd basal vein, weakly sunken above, weakly raised and darker than surface below, 1–5 mm from margin. *Inflorescences* erect to spreading; peduncle 10–35 cm long, 8–10 mm diam., 0.2–0.7× as long as petiole, green, terete; spathe reflexed, sometimes recurled, coriaceous to subcoriaceous, green to green heavily tinged with purple-violet to purplish or maroon, lanceolate to lanceolate-elliptic, 10–33 cm long, 2.5–5.5 cm wide, broadest just above the base, inserted at 30° angle on peduncle, long-acuminate at apex (the acumen inrolled), rounded to cordate at base; spadix green to purple to maroon, slightly tapered, (6)18–28 cm long, 1–2 cm diam. near base, 8–10 mm diam. near apex; flowers rhombic to weakly 4-lobed, 2.2–3.2 mm long, 2.0–3.1 mm wide, the sides weakly to jaggedly sigmoid; 10–15

flowers visible in principal spiral, 8–20 in alternate spiral; tepals matte, conspicuously punctate, minutely papillate; lateral tepals 0.8–1.6 mm wide, the inner margins broadly convex to concave when dried, the outer margins straight; pistils not emergent except when dried, green tinged with violet-purple; stigma linear, slitlike, 0.5–1 mm long; stamens emerging from the base, lateral stamens followed by alternates in rapid succession, the laterals preceding the alternates by 5–8 spirals, the 3rd stamen preceding the 4th by 6–8 spirals, held over and obscuring pistil; filaments red-violet, 1.4–1.6 mm long; anthers yellow, 0.4–0.7 mm long, 0.5–0.9 mm wide; thecae narrowly oblong to ovoid-oblong, weakly or not at all divaricate; pollen orange fading to tan or white. *Infructescence* spreading to pendent; spadix to 50 cm long, to 5 cm diam.; berries orange, oblong-ellipsoid to oblong-ovoid, acute at apex, the tip relatively blunt, to 14 mm long, 3.5 mm diam.; mesocarp with linear to punctiform raphide cells; seeds 2 per berry, oblong-ellipsoid to ellipsoid, somewhat flattened, 4.5–5 mm long, 2.7–3.2 mm diam., 1–1.5 mm thick, with a thin appendage at apex only.

Anthurium nervatum is endemic to Panama in Bocas de Toro, Coclé, Chiriquí, and Veraguas provinces at (130)500 to 2,100 m in tropical wet, premontane rain, and lower montane wet forest life zones.

This species is recognized by its long, triangular, shallowly lobed to subcordate, moderately thick leaf blades with numerous primary lateral veins, its usually long-tapered, green to maroon spadix, and by its lanceolate, coriaceous spathe that is deep maroon on the inner surface, green heavily tinged with maroon on the outer surface and often forms a loose spiral at anthesis.

Anthurium nervatum is most easily confused with *A. ranchoanum*, but that species has a shorter spadix with an erect, green spathe and larger flowers which are fewer per spiral. It may also be confused with *A. colonicum*, but that species has early exserted, acute pistils and fewer primary lateral veins.

One collection from El Valle in Coclé Province (*Croat 37443*) is probably also this species, but has a smaller, more ovate-triangular, more coriaceous blade with the posterior lobes sharply turned upward, and a deeper sinus; it also has a green rather than maroon spadix.

PANAMA. BOCAS DEL TORO & CHIRIQUÍ: Cerro Colorado, *Folsom et al. 4706* (MO); trail into Bocas and in woods on Pacific slope, from Chamí station to ca. 9 mi. along road, 1,100–1,750 m, 8°35′N, 81°54′W, *Hammel & Trainer 14919* (MO, PMA). CHIRIQUÍ: above Santa Fe along mining road 18–27 mi., off Pan-Am Hwy. above Chamí or turnoff to Escopeta, 1,200–1,500 m, *Croat 33145* (DUKE, F, MO, PMA); along mining road 31.6 km beyond bridge over Río San Félix, 10.6 km beyond turnoff to Escopeta, 1,690 m, *Croat 37177* (MO), *37169* (MO, PMA); upper mining road 20–28 mi. from San Félix, Continental Divide, 1,200–1,500 m, *Croat 33305* (MO), *33394* (MO, RSA, US); along mining road 20 mi. above bridge over Río San Félix, near village of San Félix, 750 m, *Croat 48459* (MO); Cerro Pate Macho, 1,500–1,900 m, *Stein et al. 1257* (MO); SE slopes, trail from Río Palo Alto, 4 km NE of Boquete, 1,700–2,100 m, *Sytsma et al. 4830* (MO). COCLÉ: Cerro Caracoral, *Duke & Dwyer 15118* (NY), *Kirkbride 1096* (MO, NY); Cerro Moreno, Molejón-Coclecito, 13 km NW of Cascajal, 130–250 m, 8°46′44″N, 8°31′54″W, *Davidse & Hamilton 23713* (B, MO); El Copé Region, Alto Calvario, 800–900 m, *Folsom & Jaslon 2691* (MO); El Copé, W of sawmill, *Hammel 2408* (MO); Continental Divide, lumber road N of El Copé, 10 km above El Copé, 2.2 km N of sawmill, 750–930 m, *Croat 44717, 49169* (MO, PMA); El Valle Region, El Valle de Antón, La Mesa, *Croat 37443* (CAS, CM, F, LE, KYO, M, MO, PMA, US). VERAGUAS: Santa Fe Region, vic. Escuela Agrícola Alto Piedra, 500–735 m, *Croat 33987* (CAS, MO, US), *34244* (MO, PMA), *Croat & Folsom 34134* (MO); 1,150–1,450 m, *McPherson 12070* (MO); Cerro Tute, 750–1,450 m, *Croat 48912, 48925* (MO, PMA), *Knapp & Dressler 5415* (MO, US), *5446* (MO), *Knapp & Kress 4369* (MO), *Knapp & Sytsma 2475* (MO), *Sytsma et al. 4590* (MO); Río Tercero Brazo, beyond school 500–700 m, *Croat 27329* (F, K, MO, PMA, US).

Anthurium nizandense Matuda, Bol. Soc. Bot. Mexico 24: 35, fig. 1. 1959. TYPE: Mexico. Oaxaca: Nizanda near the Isthmus of Tehuantepec, 16°40′N, 95°02′W, *MacDougall s.n.* (holotype, MEXU). Figures 207, 208.

Anthurium kruseanum Matuda, Anales Inst. Biol. Univ. Nac. Mexico 36: 107, fig. 1. 1966. TYPE: Mexico. Guerrero: La Junta (at junction of Río Omitlán and Río Papagayo) S of Tierra Colorada, *Kruse 881* (holotype, MEXU).

Usually terrestrial or epilithic; leaf scars 0.7–1.2 cm high, 1.3 cm wide; roots moderately numerous, descending, greenish to tan, smooth to somewhat pubescent, moderately elongate, tapered; cataphylls subcoriaceous, 3–7 cm long, rounded and minutely apiculate at apex, drying dark brown, persisting semi-intact, eventually as a reticulum of fibers. *Leaves* erect-spreading; petioles 6–24 cm long, (3)5–6 mm diam., quadrangular to D-shaped to subterete, flattened to broadly and sharply sulcate adaxially, the margins sharply raised, rounded abaxially, the surface pale-speckled, sometimes tinged with red-violet; geniculum slightly paler and thicker than petiole, 1–1.5 cm long; blades subcoriaceous, obovate-elliptic to elliptic, acute to abruptly acuminate at apex (the

acumen apiculate), rounded to acute or attenuate at base, 25–57 cm long, 10.7–30 cm wide, broadest at or above the middle, the margins weakly undulate; upper surface matte to semiglossy, medium green, lower surface matte, paler below; both surfaces with short, linear raphide cells and convexly raised epidermal cells, drying brown to greenish brown; midrib acutely to convexly raised above, more prominently so below; primary lateral veins 6–11 per side, departing midrib at 50–80° angle, straight to weakly arcuate-ascending to the collective vein, raised above and below, darker than surface below; tertiary veins obscure above, weakly visible below; collective vein arising from about the middle of the blade or near the apex, 3–9 mm from margin. *Inflorescences* erect, equalling or longer than leaves; peduncle 31–60 cm long, 5–8 mm diam., 1.8–2.7× as long as petiole, terete; spathe reflexed, subcoriaceous, green, ovate-lanceolate, 8–9.5 cm long, 2.5–3 cm wide, broadest near the base, inserted at 45° angle on peduncle, acute at apex, apparently obtuse at base; spadix pale green becoming reddish brown, somewhat tapered, 12–14 cm long, 9–11 mm diam. near base, 4 mm diam. near apex; flowers rhombic, 1.8–2.5 mm long, 2.8–3 mm wide, the sides sigmoid; 7–9 flowers visible in principal spiral, 5–6 in alternate spiral; lateral tepals 1.5 mm wide, the inner margins broadly convex or weakly concave; pistils not emergent; stigma broadly ellipsoid; stamens emerging rapidly in a complete sequence, emerging shortly above the tepals, arranged in a circle around the pistil; anthers ca. 0.4 mm long, 0.6 mm wide; thecae ellipsoid, weakly divaricate. *Infructescence* pendent; spathe withered; spadix 6.5 cm long, 1.5 cm diam.; berries greenish white, ovoid, 8 mm long; mesocarp transparent, juicy, pulpy; seeds 1(2) per berry, pale yellow (B & K yellow 9/2.5), broadly obovoid, 5.2–5.4 mm long, 4.5–4.7 mm diam., 3.4–4 mm thick, with a minute, translucent appendage, ± gnarled at apex on side, tinged with brown, enveloped by gelatinous substance.

Anthurium nizandense is endemic to Mexico in southern Guerrero and southern Oaxaca, where it occurs at less than 850 m in seasonally very dry habitats on steep, rocky cliffs in "selva baja caducifolia." It is known only from the vicinity of Tierra Colorada in Guerrero and Nizanda in Oaxaca.

This species is recognized by its greenish white berries and thick, narrowly to broadly elliptic or oblanceolate-elliptic, relatively long-petiolate leaves that are matte on the lower surface and sometimes exhibit a dense array of minute, linear raphide cells on drying. The epidermal cells on both surfaces of the blade are convexly raised. Matuda reported the petiole to be subquadrangular, but this was possibly due to a misinterpretation of the dried specimen since this feature is not apparent on live material.

In the area of Mexico where it occurs, *A. nizandense* could be confused only with *A. schlechtendalii* subsp. *jimenezii*, which occurs in similar habitats and is more generally abundant. *Anthurium nizandense* is distinguished by its proportionally longer petioles and its more typically elliptic blade, which is distinctly matte on the lower surface. In *A. nizandense* the blades are 1.3–2.5 times longer than the petioles. In *A. schlechtendalii* subsp. *jimenezii*, the leaf blades are usually semiglossy beneath and usually 6–10 times longer (rarely as little as 3 times longer) than the petiole.

MEXICO. GUERRERO: Río Omitlán, bridge over Río Omitlán at confluence of Río Papagayo with Río Omitlán, 850 m, *Croat 45756* (B, BM, CM, K, M, MBM, MO, P, TEX, US); La Junta, S of Tierra Colorada, *Kruse 881* (MEXU); Tierra Colorada, *Kruse 1595* (MEXU). OAXACA: Nizanda, Isthmus of Tehuantepec, *MacDougall s.n.* (MEXU).

Anthurium obscurinervium Croat, sp. nov. TYPE: Ecuador. Cañar: along road between Azogues and El Triunfo, ca. 2 km S of Hwy. at Cedro Pampa, 800–1,000 m, 2°25′S, 79°10′W, *Croat 50914* (holotype, MO 2828745; isotypes, AAU, BM, G, K, LL, M, MICH, NY, QCA, RSA, SEL, US). Figures 203, 204.

Planta terrestris aut epiphytica; caulis ad 30 cm longis, 1.3–3.5 cm diam.; cataphyllum persistens in fibris tenuibus; petiolus (3.5)6–22 cm longus, 4–10 mm diam., acute D-formatus; lamina anguste oblongato-elliptica aut oblonga-linearis, (18)30–79 cm longa, (3.2)4–7(11) cm lata; nervis primariis lateralibus obscuribus; pedunculus 20–45 longus; spatha (2.5)3–7 cm longa, 0.7–1.7 cm diam.; spadix viridis, (1.7)4–11(15) cm longus, 3–6 mm diam.; baccae atropurpurae.

Epiphytic or terrestrial; stem to more than 30 cm long, 1–3.5 cm diam.; roots dense, short, ca. 3 mm diam.; cataphylls subcoriaceous, 4–9 cm long, acute to acuminate at apex, drying whitish (B & K yellow 9/2.5 to yellow-red 9/7.5), persisting as linear fibers. *Leaves* spreading; petioles (3.5)6–22 cm long, 4–10 mm diam., sharply D-shaped, slightly thicker than broad, sharply flattened to broadly and shallowly sulcate adaxially, the margins sharply raised to curved inward, rounded to obtusely or acutely angular, sometimes 1-ribbed abaxially; geniculum somewhat thicker and much paler to darker than petiole, 0.7–1.7 cm long; blades subcoriaceous, narrowly oblong-

elliptic to oblong-linear, long-acuminate to short-acuminate (rarely acute) at apex, attenuate to narrowly acute at base, (18)30–79 cm long, (3.2)4–7(11) cm wide, broadest at or near the middle, the margins flat, weakly revolute; upper surface semi-glossy, medium to dark green, lower surface glossy, much paler; midrib convexly raised at base, becoming acutely raised toward the apex above, prominently and acutely raised at base, becoming less pronounced toward the apex below; primary lateral veins 25–55 per side, departing midrib at 40–50° angle, straight to the collective vein, obscure and flat above and below; interprimary veins numerous, almost as conspicuous as primary lateral veins; tertiary veins drying visible; collective vein arising from the base, slightly more prominent than primary lateral veins, 4–6 mm from margin. *Inflorescences* erect-spreading; peduncle 20–45 cm long, 2–4 mm diam., 1.6–4(5.5)× as long as petiole, pale green, sometimes tinged purplish, subterete to 3–4-ribbed; spathe spreading, rarely reflexed, thin, green to pale green, sometimes tinged with purple at margins, lanceolate-elliptic to linear-lanceolate, (2.5)3–7 cm long, 0.7–1.7 cm wide, broadest near the base, short-acuminate at apex (the acumen somewhat inrolled), acute at base; stipe 2–13 mm long in front and in back; spadix medium green (B & K yellow-green 7/5) to pale green, cylindroid, scarcely tapered, curved, (1.7)4–11(15) cm long, 3–6 mm diam. near base, 2–3 mm diam. near apex; flowers 4-lobed; 2–3 mm in both directions, the sides jaggedly sigmoid, 3–5 flowers visible in principal spiral, 5–7 in alternate spiral; tepals matte, weakly and minutely papillate, droplets present at anthesis; lateral tepals 1–1.8 mm wide, the inner margins straight to broadly rounded, the outer margins irregularly 3–5-sided; pistils weakly raised, green; stigma depressed, 0.2–0.4 mm long; stamens emerging in prompt sequence from the base, the laterals preceding the alternates by 3–11 spirals, held in a tight cluster above the pistil; filaments translucent, 0.4 mm long, 0.5–0.7 mm wide; anthers creamy white, 0.6–0.7 mm long, 0.7–0.9 mm wide; thecae ellipsoid to ovoid, scarcely divaricate; pollen pale yellow fading to white. *Infructescence* erect to pendent; spathe persisting, green, or absent; spadix 7–16 cm long; berries green becoming purplish to purple-black, obovoid-ellipsoid, quadrangular at apex, 6 mm long, 5 mm diam.

A member of series *Multinervia*, *Anthurium obscurinervium* is endemic to the Pacific slope of Ecuador, at 50 to 1,330 (2,000) m, in premontane moist, premontane dry and premontane wet forest.

This species is characterized by its more or less oblong leaf blades with the primary lateral veins obscure when fresh and obscure to weakly raised on drying (hence the name), green spadix with exserted stamens, and orange berries.

Anthurium obscurinervium is most similar to *A. carchiense*, which differs in having a brownish spadix and purple to purple-black fruits.

ECUADOR. BOLÍVAR: Charquiyacu, 600 m, *Solís 6114* (F). CAÑAR: Azogues–El Triunfo, 2 km S of Hwy. at Cedro Pampa, 800–1,000 m, 2°25′S, 79°10′W, *Croat 50914* (AAU, BM, G, K, LL, M, MICH, MO, NY, QCA, RSA, SEL, US). CARCHÍ: Gualpí Chico, near Awá encampment, 1,300 m, 0°58′N, 78°16′W, *Hoover et al. 2658* (MO). COTOPAXI: Río Pilaló, Quevedo–Latacunga, 950–1,100 m, 0°53′S, 79°10′W, *Holm-Nielsen et al. 3076* (AAU). EL ORO: 11 km W of Piñas, new rd. to Santa Rosa, 850 m, *Dodson et al. 9033, 9037* (MO, SEL); Machala–Loja, 25 km SE of jct. to Piñas, 890 m, 4°15′S, 79°45′W, *Croat 50715* (CM, MO, NY, SEL, US, TEX). GUAYAS: Naranjal–Machala, 13 km S of Naranjal, 50–150 m, *Harling & Andersson 19301* (GB, MO). LOS RÍOS: Alta Centinela, 29.5 km W of Patricia Pilar, 450–475 m, 0°33′S, 79°22′W, *Croat 50664* (AAU, MO, NY, RSA); Patricia Pilar–24 de Mayo, Centinela, *Dodson et al. 8703* (MO, SEL); Río Blanco, Santo Domingo de Los Colorados–Esmeraldas, Villa Hermosa, 3 km S of Km 24, 250 m, 0°5′S, 79°15′W, *Croat 50694A* (MO). PICHINCHA: 27 km S of San Juan, 12 km NE of Chiriboga, 2,000 m, 0°17′S, 78°42′W, *Croat 50606A* (IBE, K, MO, NY, RSA, US, VDB).

Anthurium oerstedianum Schott, Oesterr. Bot. Z. 8: 180. 1858. TYPE: Costa Rica. Near Naranjo, *Oersted s.n.* (lectotype, illustrated by Schott, Aroideae 328). Figures 205, 206.

Anthurium cuspidifolium Schott, Oesterr. Bot. Z. 8: 180. 1858. TYPE: Costa Rica, *Oersted s.n.* (lectotype, illustrated by Schott, Aroideae 314).

Terrestrial; stem to 30 cm long, 2–4 cm diam.; leaf scars, 0.8–1 cm high, 2–2.5 cm wide; roots moderately numerous, descending, tan, smooth, short, moderately thick, slightly tapered, 3–5 mm diam.; cataphylls subcoriaceous, 7–13 cm long, acute at apex and with subapical apiculum, medium green, drying brown, persisting intact, eventually deciduous. *Leaves* erect to spreading; petioles (12)30–73 cm long, 5–7 mm diam., quadrangular to subterete, flattened to weakly and broadly sulcate adaxially, sharply to bluntly 1–3 ribbed abaxially, the surface minutely pale-speckled; geniculum remote from the base of the blade 10–20 cm, 1.5–2 cm long; blades subcoriaceous, ovate to narrowly ovate or lanceolate, long-acuminate at apex, abruptly attenuate then acute to obtuse to truncate or subcordate at base, 20–66 cm long, 8.5–30 cm wide, broadest at or near the middle, the mar-

gins undulate; upper surface matte to weakly glossy, medium green, lower surface semiglossy to glossy, paler; midrib bluntly angular-raised above, below prominently higher than broad at base, becoming angular-raised toward the apex and paler than surface; primary lateral veins 11–20 per side, departing midrib at 40–60° angle, broadly arcuate, sunken to weakly raised in grooves above, prominently convexly raised below; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins sunken above, raised below; collective vein arising from near the base, sunken above, raised below, equally as prominent as primary lateral veins, 2–8 mm from margin. *Inflorescences* erect, longer than leaves; peduncle (30)70–130 cm long, equal to 1.2–1.5× as long as petiole; spathe pale green, ovate-lanceolate, 8–13 cm long, 2.5–4.8 cm wide, inserted at 45° angle on peduncle, acuminate at apex, rounded at base; spadix pale green, moderately tapered, 5–12 cm long, ca. 9 mm diam. near base, ca. 6 mm diam. near apex; flowers sub-rhombic to 4-lobed, 1.7–2.5 mm long, 2–2.7 mm wide, the sides straight to sigmoid; 8–9 flowers visible in principal spiral, 12–18 in alternate spiral; tepals matte, minutely and densely papillate; lateral tepals 1.4–1.8 mm wide, the inner margins straight; pistils weakly emergent, green; stigma 0.4 mm long, weakly exserted and brush-like, droplets appearing 3–4 days before stamens emerge; stamens emerging in a scattered pattern, held against the pistil; filaments fleshy, greenish, translucent; anthers creamy white, 0.5–1 mm long, 0.6–1.1 mm wide; thecae ellipsoid, not divaricate; pollen yellow fading to creamy white, abundant.

Anthurium oerstedianum is endemic to Costa Rica at 800 to 1,300 m, principally on the southwestern, Pacific slope in premontane wet, tropical wet, and premontane rain forest.

This species is distinguished by its strictly terrestrial habit as an understory forest herb and by its geniculum, which is located 10–20 cm below the base of the blade. Other distinguishing features are its four-sided petiole and greenish spadix. This species is a somewhat atypical member of sect. *Pachyneurium* because of its elongate petioles, remote geniculum, and lack of a dense, rosulate habit. It is apparently not closely related to any other species.

Anthurium cuspidifolium, which is synonymous with *A. oerstedianum*, was reported by Macbride (1936) from Peru. However, the specimens cited by him (*Macbride 5622* (F); *Schunke 572* (F)) are referable to *A. flavescens* Poeppig.

The Cartago collection locality cited by Schott in the type description is dubious because no modern collection of this species has been made from anywhere on the Atlantic slope. Since Schott mentions only "Naranjo," perhaps the collection refers to the Río Naranjo on the Pacific slope where it easily could have occurred.

COSTA RICA. CARTAGO: vic. Naranjo, *Oersted s.n.* (illustrated by Schott, Aroideae 328). PUNTARENAS: 6 km S of San Vito de Java, Wilson's finca, 1,330 m, *Raven 20922* (MO); Las Cruces Botanical Garden, along road to river below botanical garden, 1,300 m, *Croat 44415* (MO); Osa Peninsula, Corcovado, *Gilbert s.n.* (MO). SAN JOSÉ: San Isidro de General–coastal town of Dominical, SW of San Isidro, 900–1,000 m, *Croat 35267* (MO, NY), *35293* (MO); 0.5 mi. above turnoff to Canaán at Rivas, 900 m, *Croat 43419* (MO); El General, 1,010 m, *Skutch 2291* (MO); Cerro Pelón, N base, just E of main road, 0.5 km S of San Martín de Puriscal, 800 m, 9°44′N, 84°23′W, *Grayum & Baker 4693* (B, CR, MO); Río Chirripó del Pacifico, Canaán–Chimirol, General Valley, 1,000 m, *Burger & Liesner 7124* (MO).

Anthurium ottonis K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem XI: 609. 1932. TYPE: Bolivia. La Paz: Prov. Sud Yungas: Jirupaysi, near Yanacachi, *Buchtien 387* (holotype, B). Figures 209, 210.

Terrestrial; stem moderately slender, to at least 11 cm long, 0.8–1.5 cm diam.; roots moderately numerous, spreading, green, drying grayish to pale brown, ± villous, especially when young, elongate, somewhat tapered, sometimes branching, ca. 3–25 cm long, 2–8 mm diam.; cataphylls subcoriaceous, lanceolate to broadly lanceolate, 7–13 cm long, acute to rounded at apex, yellow-green, tinged with red, drying brown to reddish brown (B & K yellow-red 4/10), persisting intact to semi-intact, rarely as fine linear fibers, eventually deciduous. *Leaves* erect to spreading; petioles 22–42 cm long, 3–6 mm diam., erect to erect-spreading, subterete to broader than thick, bluntly and shallowly sulcate adaxially, rounded abaxially, the surface prominently pale-speckled; geniculum much paler and somewhat thicker than petiole, becoming fissured transversely with age, 0.5–2 cm long; blades coriaceous, linear-oblong, narrowly acute and mucronate at apex, acute to obtuse to narrowly rounded at base, 38–60(100) cm long, 2.2–7 cm wide, broadest at or near the middle (12.6–17.6× longer than the petiole), the margins flat to somewhat undulate; upper surface matte to weakly glossy, dark green, lower surface matte, conspicuously paler; both surfaces drying matte, green to yellowish green; midrib convexly raised, paler than surface above, pale-speckled like petiole, higher than broad at base, becoming prominently convex to-

ward the apex below, moderately paler than surface and pale-speckled like petiole; primary lateral veins 18–26 per side, departing midrib at 45–60° angle, straight to arcuate, weakly sunken to obscure above, darker than surface below; interprimary veins obscure above, almost as conspicuous as primary lateral veins below; tertiary veins obscure above, weakly visible below; reticulate veins not visible; collective vein arising from the base, equally as prominent as primary lateral veins, 1–4(6) mm from margin. *Inflorescences* erect, shorter than leaves; peduncle 27–50 cm long, 2–4 mm diam., 0.8–1.3× as long as petioles, pale reddish, drying greenish to brownish, terete; spathe spreading-recurled, subcoriaceous, yellow-green tinged with red on the midline, oblong-lanceolate to linear, ca. 3.5–6.5 cm long, 0.8–1.3 cm wide, broadest near the base, acute to abruptly acuminate at apex (the acumen apiculate, 4 mm long), acute at base; spadix maroon (B & K red-purple 2/5), dark brown when dried, slightly tapered, subsessile, somewhat curved, held at 150° angle from peduncle, 4–10(12) cm long, 4–5(6) mm diam. near base, 2–3 mm diam. near apex; flowers ± square to almost 4-lobed, 2–2.4 mm in both directions, the sides ± straight to jaggedly sigmoid; 3–6 flowers visible in principal spiral, 6–9 in alternate spiral; tepals matte, very minutely and densely papillate, punctate, with few droplets appearing as stamens emerge; lateral tepals 1–1.2(2) mm wide, the inner margins straight to convex, the outer margins 2- rarely 3-sided; pistils semiglossy, minutely papillate, emergent before stamens emerge, dark maroon; stigma ellipsoid, 0.3–0.7(0.9) mm long, depressed medially; stamens emerging in a regular sequence from the base, arranged shortly above the tepals, the laterals preceding the alternates by 14–15 spirals, held in a circle around the pistil; anthers white, drying white to brown, 0.5–0.7 mm long, 0.6–1 mm wide; thecae ovoid, not divaricate; pollen white. *Infructescence* not seen.

A member of series *Multinervia*, *Anthurium ottonis* is known from Bolivia in the Department of La Paz and in Puno, Peru, at 890 to 1,700 (2,500) m in lower montane subtropical moist, lower montane subtropical wet, and subtropical moist forest life zones.

This species is distinguished by its erect-spreading leaves, long, pale-speckled, subterete petioles and narrowly straplike blades, and long-pedunculate inflorescence with a moderately stubby, maroon spadix. It is not confused with any other *Pachyneurium* species and apparently has no close relatives. Although on the majority of dried specimens the anthers appear orange to brown, the type specimen displays white-drying anthers.

A collection (*Bogner 903*) cultivated at the Munich Botanical Garden and represented by two sheets at the Kew Herbarium is similar to *A. ottonis* in most respects, except that it has a prolonged, free-ending sheath 4–11.7 cm long. It may represent a new species.

BOLIVIA. LA PAZ: Prov. Inquivisi, Inquivisi–Circuata, 2,500 m, *Besse et al. 656* (SEL); Prov. Loayza, Circuata–Miquilla, Km 28, 1,560 m, *Besse et al. 1839* (SEL); Prov. Nor Yungas, Coroico, Polo–Polo, 1,100 m, *Buchtien 3659, 3661* (US), *3660* (GH, US), *3662* (HBG, US); Coroico (Yolosa jct.)–Caranavi, road parallel to Río Coroico, 670–1,280 m, *Davidson 4790* (MO); Río Huarinilla, 4.5 km below Yolosa, then 14 km W on road up Río Huarinilla, 1,200–1,300 m, 16°12′S, 67°50′W, *Solomon 9390* (MO); below Yolosa, 1,450 m, *Solomon 8652* (B, MO); Prov. Sud Yungas, 15 km toward Irupana, Chulumani, 1,700 m, *Beck 4724* (K, M, MO); Yanacachi, Jirupaysi, 1,650 m, *Buchtien 387* (B); Chulumani, 50 km towards Asunta, 890 m, *Beck 12606* (MO); 26 km towards Asunta, past Tajama, 1,300 m, *Beck 12074* (MO). PERU. CUZCO: Urubamba, Machupicchu, 2,000 m, *Bogner 903* (K). PUNO: San Gavón, *Baker 4358* (cultivated at MO) (MO, NY).

Anthurium oxycarpum Poeppig in Poeppig & Endl., Nov. Gen. Sp. 3: 83. 1845. TYPE: Peru. Loreto: Yurimaguas, *Poeppig s.n.* (lectotype, selected here, G). Figures 211–213.

Anthurium strictum N. E. Br ex Engl., Monogr. Phan. 2: 638. 1879. TYPE: Brazil. Acre: Rio Branco, *N. E. Brown s.n.* (K, identified with Kew Negative #2805).

Epiphytic or terrestrial, sometimes epipetric; stem short or elongate, to 60 cm long, 1–3 cm wide; leaf scars inconspicuous, obscured by root mass, 1 cm high, 1.2 cm wide; roots numerous, dense, spreading, green to whitish, smooth to densely pubescent when dried, short, bluntly tapered, 1–7.5 cm long, (1)2–4 mm diam.; cataphylls membranous to subcoriaceous, lanceolate, prominently 1-ribbed throughout, 5.5–12 cm long, acuminate at apex with subapical apiculum 1–2 mm long, light green, drying thin, yellowish to pale tan (B & K yellow 7/5), persisting ± intact, eventually as fine linear fibers. *Leaves* erect to erect-spreading; petioles (2.5)5–15 cm long, 4–9 mm diam., subterete to C-shaped to D-shaped, flattened to narrowly or obtusely sulcate adaxially, the margins blunt, rounded abaxially, the surface dark green, pale-speckled; geniculum slightly thicker than petiole, 1–2.5 cm long; sheath for 3–4 cm long; blades subcoriaceous, narrowly to broadly elliptic to broadly oblanceolate to narrowly obovate, acute to short-

acuminate at apex (the acumen downturned, inrolled), obtuse to acute or attenuate at base, (12)22–55 cm long, 10–19 cm wide, broadest at or above the middle, the margins flat to broadly undulate; upper surface glossy to semiglossy, occasionally matte, medium to dark green, lower surface matte to weakly glossy, moderately to conspicuously paler; midrib above raised and paler than to concolorous with the surface, below prominently and obtusely to acutely raised at base, becoming convexly raised toward the apex and slightly paler than surface; primary lateral veins 10–25 per side, departing midrib at 40–70° angle, straight to weakly arcuate to the collective vein, weakly raised near the midrib, becoming sunken in grooves toward the margin; interprimary veins weakly sunken above, weakly raised below; tertiary veins weakly sunken above, raised below; reticulate veins obscure; collective vein arising from near the base, sunken above, raised below, paler than surface, 5–11 mm from margin. *Inflorescences* erect, equaling or longer than leaves; peduncle 18.5–54.7 cm long, 3–5 mm diam., 2.5–5× as long as petiole, green, terete; spathe spreading to reflexed at an acute to almost right angle from spadix, coriaceous to subcoriaceous, light to dark green, sometimes tinged with red or maroon at margins, lanceolate to ovate-lanceolate, sometimes elliptic, 4.5–12.5 cm long, 1–3 cm wide, broadest usually in the lower third (sometimes at or near the middle), inserted at 35–45° angle on peduncle, abruptly acuminate at apex (the acumen tightly inrolled, 6 mm long), acute to acuminate at base, the margins meeting at 60–80° angle; stipe to 17–20 mm long in front, 0–1 mm long in back; spadix bluish green to green to yellow-green, also reported as creamy and tan, tapered, erect, held at 140–170° angle from peduncle, 4–8.5 cm long, 6–10 mm diam. near base, 3–7 mm diam. near apex; flowers square, 2.4–3.2 mm in both directions, the sides moderately straight parallel to spiral, straight to jaggedly sigmoid perpendicular to spiral; 4–7 flowers visible in principal spiral, 9–11 in alternate spiral; tepals covered with thin, matte, bluish green, waxy bloom, few droplets present at anthesis; lateral tepals 1.3–2 mm wide, the inner margins broadly convex, the outer margins 2–3-sided; pistils weakly emergent at anthesis, matte covered with waxy bloom, green, becoming brown; stigma oblong-ellipsoid, 0.6–0.7 mm long, brushlike and depressed medially before droplets emerge; stamens emerging in a prompt, regular, complete sequence from the base, inclined slightly inward over the stigma; anthers creamy white to orange, 0.5–0.6 mm long, 0.6–0.8 mm wide; thecae oblong-ovoid, scarcely divaricate; pollen white. *Infructescence* with spathe persisting; spadix 6.5–8.5 cm long, 1.8–2.5 cm diam., with berries scattered throughout; berries green, becoming red and eventually purple in the apical half, obovoid-oblong to ellipsoid-obovoid, long-acuminate toward the apex, rounded at apex with radial ridges, 7.5–12.3 mm long, 4.2–5 mm diam near base, toward the apex narrowing to 1.7–2.5 mm diam.; pericarp thin, transparent; mesocarp gelatinous with moderate number of raphide cells; seeds 2 per berry, yellowish, oblong-ovoid, flattened, 5.3–5.5 mm long, 3 mm diam., 1.5–1.8 mm thick, enveloped by transparent, sometimes amber, gelatinous, sticky substance.

Anthurium oxycarpum ranges from southeastern Colombia to Amazonian Ecuador, Peru, Bolivia, and Brazil at 100 to 870 (1,300) m. It occurs in tropical moist, premontane wet and tropical wet forest life zones.

This species is distinguished by its rosulate habit, generally short, densely short-rooted stem, conspicuously veiny leaves (with at least some of the tertiary veins sunken above), and especially by its erect, narrowly ovate-lanceolate spathe and frequently bluish green, slightly tapered spadix. The leaf blades characteristically dry thin and somewhat glossy on the lower surface. Some cultivated plants of this species have markedly bullate and weakly quilted leaf blades, a characteristic not yet observed in the field.

Anthurium oxycarpum is closest to *A. knappiae*, which differs in having petioles two to three times longer, an attenuate leaf base, a much longer peduncle, a nonglaucous spadix, and tepals with conspicuous raphide cells. See discussion of that species for details.

The original type specimen designated by Poeppig was collected in Brazil at Ega (now Tefe), located on the Rio Solimoes at the mouth of the Rio Japurá. Originally deposited at Vienna, this specimen is now lost, and a thorough search of all major herbaria has turned up no duplicates. Consequently, a second Poeppig collection from Yurimaguas in Peru, cited by Engler in his 1905 revision, is here designated as the lectotype. The Yurimaguas collection is also the only one illustrated by Schott (Scott drawing 356; NYBG Negative #3873; microfiche #15: C-7).

Considerable confusion exists regarding the type of *Anthurium strictum*, now a synonym of *A. oxycarpum*. In preparing a description of what he presumed to be *A. dombeyanum* for the Refugium Botanicum, Baker (1871) described and illustrated instead *A. oxycarpum*. Upon realizing this error

and assuming the latter to be a new species, Engler (1879) redescribed it as *A. strictum*, attributing the name to N. E. Brown at Kew. He cited as the type the same material used to illustrate the Refugium Botanicum article, namely a specimen from the Rio Branco in Brazil (at least an inflorescence of the type specimen had been sent to Engler in Berlin by N. E. Brown).

Engler also misidentified as *Anthurium strictum* an Ule collection (*5598*) from western Acre along the Rio Jurua Mirim. While photographing type specimens in Berlin, J. F. Macbride of the Field Museum incorporated into a single photograph an inflorescence of *A. oxycarpum* (labeled *A. strictum*) with the Ule collection misidentified by Engler. The latter collection, which is complete, is actually *A. uleanum*. The mixed collection represented in this Field Museum photograph needs to be corrected. The specimen to the left represents *A. uleanum*, while the one to the right (inflorescence only) represents *A. oxycarpum*.

BOLIVIA. EL BENI: Rurrenabaque, *Cárdenas 1167* (NY); Prov. Ballivian, Misión Fátima Río Maniqui, *Canchi & Hinojosa 1045* (LPB, MO). LA PAZ: Prov. Larecaja, 27.8 km N of Caranavi, *Croat 51651* (MO); Prov. Sud Yugas, Alto Beni Concesión de la Cooperación de San José de Popoy, 600 m, *Seidel & Schulte 2246* (LPB, MO). BRAZIL. ACRE: Abuña–Rio Branco, *Forero et al. 6315* (COL, NY, US, INPA); Rio Branco, Zoobotanical Garden of Federal University of Acre, *Lowrie et al. 170* (INPA, MG, MO, NY); Mpo. Caramari Amazonas, Rio Juruá, N of Cruzeiro do Sul, Lago da Cigana (São Luis), S of Porto Alvaro Nestrinho, 150 m, 7°37′S, 72°36′W, *Croat 62498A* (CM, INPA, MO); Rio Juruá Mirim, *Ule 5598* (B). AMAZONAS: Rio Javarí, behind Estirão de Equador, *Lleras et al. P17284* (INPA, NY); Rio Purus, Monte Verde, *Huber 4623* (MG). RONDÔNIA: NW of Rio Madeira, across from Matuparana, *Calderón et al. 2828* (MO, NY, US); Mpo. Ariquemes, Mineracão Mibrasa, sector Alto Candeias, Km 128, 10°35′S, 63°35′W, *Teixeira et al. 467* (NY, INPA). COLOMBIA. Without locality, *Fantz 4032* (FTG). AMAZONAS: Leticia, *Krukoff 5144* (NY), *Oldenburg 2812* (US); Río Loretoyacu, 100 m, *Schultes & Black 8407* (US, GH); Puerto Nariño, 100 m, *Plowman 3221* (GH, US, SEL), *Madison 3743* (cult. plant of *Plowman 3221* (SEL). ECUADOR. MORONA-SANTIAGO: 20 km from Limón, 700–900 m, *Harling & Andersson 12875* (GB). NAPO: Reserva de Producción Faunística Cuyabeno, N of Laguna Grande, 265 m, *Nielsen 76226, 76516* (AAU), *Poulsen 79692* (AAU); Puerto Napo–Puerto Misahuallí, 3.5 km E of Puerto Napo, 1°2′S, 77°47′W, *Croat 58882* (C, CAS, CM, GH, MO, NY, QCA, RSA, SEL); 8 km below Puerto Misahuallí on Río Napo, 1.5 km S, 1°4′S, 77°36′W, 450 m, *Palacios et al. 404* (MO, QCNE), *Palacios 2859, 2877* (MO), *2961* (MBM, MO, QCNE, W); Lago Agrio–Coca, 8.8 km S of Río Aguarico on road to Coca, San Francisco de Orellana, *Croat 58512A* (MO); confluence of Río Borja and Río Quijos, E bank, ca. 1,300 m, 0°25′S, 77°49′W, *Holm-Nielsen et al. 26234* (AAU); Río Aguarico, *Holm-Nielsen et al. 21115* (AAU, UEC); 30 min. by canoe below San Pablo, 250 m, 0°18′S, 76°25′W, *Laegaard 51563* (QCA); Río Arajuno, Sola Cocha, 500 m, 1°7′S, 77°36′W, *Palacios et al. 896* (MO); Río Lagartococha, 190 m, 0°33′S, 75°13′W, *Lawesson et al. 44409* (AAU); Río Napo, Limoncocha, 240 m, *Foster 3839* (F), *Madison et al. 5432* (MO, SEL, QCA, US, K); Jatún Sacha Biological Reserve, 8 km below Misahuallí, 450 m, 1°04′S, 77°36′W, *Cerón 723, 1312* (MO), *Cerón et al. 1992* (MO, QCNE); 400 m, *Cerón 6289* (MO, QCA), *5963* (KRAM, MO, OOM); Río Wai si aya, 1 km upstream from Río Aguarico, *Brandbyge et al. 33190* (AAU); NAPO–PASTAZA: Tena, *Asplund 9199* (S); Tena–Napo, *Asplund 10253* (S). PASTAZA: Río Curaray, Curaray, 200 m, *Harling & Andersson 17517* (GB). PERU. AMAZONAS: Prov. Bagua, Río Cenepa, Pagat, *Kayap 422* (DUKE, MO). AYACUCHO: Río Apurimac, Kimpitiriki, 400 m, *Killip & Smith 23021* (US). HUÁNUCO: Tingo María Region, Prov. Leoncio Prado, 5 km S of Tingo María, Route 16, 870 m, *Davidson 3424* (MO, LAM); E of Tingo María, *Barbour 20476* (US); Las Palmas–Tingo María, 720 m, *Madison 6743* (QCA, SEL); Puente Durán, *Plowman & Kennedy 5699* (SEL, MO); Río Monzón, *Schunke 5111* (GH, F, US, NY); Jacintillo, W of Tingo María, 800 m, *Plowman & Kennedy 5772* (F, GH); Quebrada Las Pavas, 5 km N of Tingo María, 720 m, *Plowman & Kennedy 5708* (GH); W of Tingo María, Cerro Quemado, 700–800 m, *Schunke 10438* (AAU, BM, MO, NY, RSA, U, US), *10602* (MO); Dtto. Ruppa Ruppa, Carpar Bella, Cave of Los Huarinos, 700–900 m, *Schunke 9465* (CAS, CM, F, G, MO); Río Huallaga, 750–800 m, *Plowman & Ramirez 7569* (F); Tingo María–Monzón, Río Patay Rondos, 650 m, 9°21′S, 76°12′W, *Croat 57946* (CM, MO). JUNÍN: Puerto Bermúdez, 375 m, *Killip & Smith 26604* (US, NY); Oserato Tambo, *Weiss 152* (F); Río Leco, *Soukup 3516* (F); Río Perene, mouth of river, *Weberbauer 11920* (USM). LORETO: Iquitos, road to Quisto Cocha, 100 m, *Plowman 2585* (F, GH); Prov. Alto Amazonas, Andoas, 180 m, 02°55′S, 76°25′W, *Vásquez & Jaramillo 4566* (MO); Río Huallaga, Santa Rosa, below Yurimaguas, 135 m, *Killip & Smith 28714* (NY, US); Yurimaguas, 135 m, *Killip & Smith 28014* (NY, US, F); Yurimaguas–Balsapuerto, 135–150 m, *Killip & Smith 28367* (US); Río Huallaga (lower basin), Balsapuerto, 150–350 m, *Killip & Smith 28628* (US, NY); Río Napo, Entrada de Isla Inayuga, *Croat 20549* (MO); Prov. Coronel Portillo, Caserío de J. C. Mariategui and Mejico, 300 m, 8°15′S, 73°45′W, *Diaz et al. 756* (MO); Prov. Maynas, Iquitos Region, Soledad, Río Itaya, 110 m, *Killip & Smith 29762* (NY, US); Río Amazonas, Explorama Inn, 1 km S of Indiana, 130 m, 3°30′S, 73°01′W, *Croat 61679* (AMAZ, MO), *Gentry et al. 54623* (MO), *55986* (MO), *61772* (MO), *65765* (MO, TEX), *65805* (MO, SAR); 106 m, *Vásquez et al. 12152* (MO); Indiana–mouth of Río Napo, 130 m, 3°28′S, 72°48′W, *Gentry et al. 31429* (MO); Iquitos Region, Las Pebas, Río Ampiyacu, Pijuayal Army Base, 3°10′S, 71°49′W, *Plowman et al. 7131* (F, GH); Indiana–mouth of Río Napo, Yanamono, 130 m, 3°28′S, 72°50′W, *Croat 61739* (AMAZ, MO), *Gentry et al. 27509, 39713, 42256* (MO), *Gentry & Jaramillo 28062* (MO), *Gentry & Vásquez 42296* (MO); Dtto. Mazán, Río Amazonas–Mazán, 100–150 m, *Rimachi 212* (IBE, MO); Veradera de Mazán, *Croat 19428* (F, MO, USM), *20779, 20789* (MO); Prov. Requena, Sinchicuy, 106 m, 3°35′S, 73°15′W, *Vásquez et al. 7830* (MO). MADRE DE DIOS: Prov. Manú, Manú National Park, Cocha Cashu Biological Station, 350–400 m, *Foster 9902* (B, K, MO), *Gentry 2720* (MO), *43638*

(MO, SEL), *Nuñez 5537* (MO), *5738* (MO, W), *5809* (MO, US); Río La Torre, confluence of Río Tambopata and Río La Torre, 39 km SW of Puerto Maldonado, 12°50′S, 69°20′W, *Barbour 4767, 5424* (MO), *Smith et al. 132* (MO, US), *346* (US), *1387, 1391* (US). PASCO: Prov. Oxapampa. Palcazú Valley, Iscozazin, 380 m, 10°12′S, 75°15′W, *Foster et al. 7841* (MO); Río San José, Río Chuchurras drainage, 400–500 m, 10°09′S, 75°20′W, *Smith 4037* (MO). UCAYALI: LSU base camp, Quebrada Shesha (trib. of Río Abajao), 65 km NE of Pucallpa, 250 m, 8°02′S, 73°55′W, *Gentry & Díaz 58559* (MO).

Anthurium oxyphyllum Sodiro, Anales Univ. Centr. Ecuador 15(108): 5. 1901. TYPE: Ecuador. Pichincha: near Santo Domingo de Los Colorados, 400 m, *Sodiro s.n.* (holotype, Q). Figures 214–216.

Epiphytic; stem short, (1)1.5–2 cm diam.; roots dense, numerous, ascending to spreading, green, smooth when young, soon becoming tomentose, slender and elongate, to 13 cm long, 2–6 mm diam.; cataphylls membranous, 7–10 cm long, narrowly rounded at apex with subapical apiculum ca. 8 mm long, drying tan (B & K yellow 9/2.5), persisting as fine linear fibers. *Leaves* spreading; petioles 6–25(30) cm long, 4–7 mm diam., D-shaped, flattened to convex to weakly sulcate or occasionally with a medial rib adaxially, the margins sharply raised, rounded abaxially; geniculum thicker and paler than petiole, (0.7)1–2 cm long; blades coriaceous, narrowly elliptic to sometimes narrowly oblanceolate, long-acuminate at apex (the acumen flat), long-attenuate at base, 45–70 cm long, (4)6–11 cm wide, broadest at or near the middle, the margins broadly undulate; upper surface matte, dark to bright green, lower surface glossy to semiglossy, paler; both surfaces drying matte, greenish to yellowish brown; midrib flat to convexly raised above, prominently and acutely raised and paler than surface below; primary lateral veins 25–35 per side, departing midrib at 30–60° angle, ± straight to the collective vein, scarcely raised to flat or weakly sunken above, weakly raised to ± obscure below, drying slightly raised above and below; interprimary veins numerous, almost as conspicuous as primary lateral veins, obscure when fresh, weakly raised when dried; tertiary veins visible when dried; collective vein arising from near the base, equally as prominent as primary lateral veins, raised when dried, 3–6 mm from margin. *Inflorescences* pendent to erect-spreading, shorter than leaves; peduncle (21)24–46 cm long, (3)4–5 mm diam., 1.2–6× as long as petiole, light green tinged with purple or maroon at least at base, terete to subterete and flattened adaxially; spathe deflexed to reflexed, held at 130–160° angle to peduncle, often weakly twisted, subcoriaceous, green to green tinged with purple or red (B & K yellow-green 7/10), lanceolate to oblanceolate, (5)7.2–10.5 cm long, (1.8)2.3–3 cm wide, broadest near the base, inserted at 30–90° angle on peduncle, abruptly acuminate at apex (the acumen inrolled), obtuse to rounded at base, the margins meeting at 100–140° angle; stipe 3–7 mm long or absent; spadix green to yellow-green (B & K yellow-green 6/10), cylindroid, semi-erect to nodding, usually slightly curved, held at (150)130–60° angle from peduncle, 5.8–11 cm long, 3–7 mm diam. near base, 3–5 mm diam. near apex; flowers ± rhombic to 4-lobed, 3–4.5 mm long, 3.7–4.3 mm wide, the sides straight to smoothly or sometimes jaggedly sigmoid; 5–7 flowers visible in principal spiral, 6–8 in alternate spiral; tepals brown, matte to semiglossy, minutely papillate, with abundant droplets present; lateral tepals 1.3–2.5 mm wide, the inner margins broadly convex to straight, scarcely turned up against the pistil, the outer margins 2-sided; pistils prominently emergent, exserted and papillate, the exposed portion squarish, green becoming dark purple; stigma linear to ellipsoid, ca. 0.4 mm long, weakly raised, copious droplets appearing before the stamens emerge; stamens emerging in a regular sequence throughout, held well above the tepals, lateral stamens emerging almost to apex before alternates begin to emerge, arranged in a circle around the pistil; filaments transparent, prominently exserted, thin and flattened, 1.5–1.7 mm long; anthers orange, becoming pinkish or reddish brown, ca. 0.8 mm long, 0.9 mm wide; thecae oblong-ellipsoid, scarcely divaricate; pollen orange, fading to white or tan. *Infructescence* with spathe persisting; spadix 9.5–11.5 cm long, 1–1.5 cm diam., with berries scattered throughout; berries orange, ellipsoid, acute and with radial ridges at apex, 6.8–7 mm long, 3.2–3.7 mm diam.; mesocarp mealy; seeds 1 per berry, yellow-brown when dried, ± ovoid, truncate at both ends, 3.5–5 mm long, 2.2–3 mm diam., 1.5–1.6 mm thick, enveloped by gelatinous, translucent, amber substance.

A member of series *Multinervia*, *Anthurium oxyphyllum* is endemic to the Pacific slope in Ecuador from Carchí to Cotopaxi at 300 to 1,300 m. This species is ecologically variable, with specimens collected both in a lower montane dry forest life zone (Esmeraldas) and a montane rainforest life zone (Carchí). Despite occurring in different life zones, the specimens themselves do not differ significantly in any aspect. However, the type col-

lection is somewhat unusual in having leaf blades with apices cuspidate-acuminate rather than long-acuminate.

This species is characterized by its epiphytic habit, generally oblong-elliptic, coriaceous, greenish-drying blades with numerous primary lateral and interprimary veins, long peduncles (1.2–6× longer than the petioles) and flowers with prominently exserted stamens. However, the best distinguishing character is the nodding inflorescence with the spathe and spadix abruptly bent downward at the base.

Anthurium oxyphyllum bears some resemblance to *A. carchiense* and *A. obscurinervium*, both of which have less coriaceous leaf blades and erect inflorescences.

Sodiro (1902) asserts that the leaf blades are not punctate, but rather "pellucid-punctate under a lens." This agrees with living material, in which the leaf blades cast a semi-"velvety" sheen when held at arm's length. This effect results from modified epidermal cells ("pellucid punctations") which scatter light in different directions. Most of Sodiro's descriptions were based on living material, and this observation was probably made on a living plant.

ECUADOR. CARCHÍ: Chical, 1,130 m, 0°56′N, 78°14′W, *Hoover & Wormley 1402* (MO); Río San Juan, Chical, 12 km below Maldonado, 1,200 m, 1°4′N, 78°17′W, *Madison et al. 4507* (K, SEL, F); Peñas Blancas, 20 km below Maldonado, 1,100 m, *Madison 6967* (SEL); Gualpi Chico, Forestry Reserve, vic. of encampment at Awá Ethnic, 1,330 m, *Hoover et al. 3256* (MO). COTOPAXI: Quevedo–Latacunga, 55.5 km from Quevedo, 23.5 km E of La Maná, 930–950 m, 0°53′S, 79°4′W, *Croat 57056* (CM, MO). ESMERALDAS: less than 300 m, *Cobb 72* (MO); Ibarra–San Lorenzo, Lita, 550–650 m, *Madison et al. 4992* (SEL, K, QCA), *5141*, *5199* (SEL), *Croat 69736* (cultivated at MO); Lita, 600–650 m, *Maas & Cobb 4743* (U, QCA). IMBABURA: vic. Lita, 600 m, *Cobb 35* (MO); Río Mira, Ibarra–Lita, 2.5 km E of Lita, 750–775 m, *Croat 38977* (M, MO, RSA, SEL).

Anthurium pachylaminum Croat, sp. nov. TYPE: Peru. San Martín, Moyobamba–Chachapoyas, Km 430–431, E of Naranjos at Río Naranjos, 770 m, 5°21′S, 77°20′W, *Croat 58161* (holotype, MO 3148985; isotypes AAU, B, CAS, F, GH, K, M, NY, P, SEL, U, US, USM). Figures 217–220.

Planta epiphytica; petiolus sulcatus, 8–20(32) cm longus; lamina elliptica aut late elliptica vel oblanceolata, 40–112 cm longa, (11)17–43 cm lata, acuminata, basi acutata et interdum decurrenti, in pagina inferior pustulata vel aliquando glandulosa; nervii primarii laterales 6–9 utroque; pedunculus 36–95 cm longus, 2–9 plo longior quam petiolus; spatha subcoriacea, linearis-lanceolata, 10–23 cm longa, 1–2.5 cm lata; spadix atrorubens vel atroviolaco-atropurpurea, cylindricus, 11–39 cm longus; cum fructu pendulus; baccae ferentes ad basim.

Epiphytic, sometimes terrestrial; stem to 8 cm long, 1.5–6 cm diam.; roots numerous, dense, spreading, the uppermost ascending, gray when dried, drying short-pubescent, 2–10 cm long, 2–5 mm diam.; cataphylls coriaceous to subcoriaceous, broadly lanceolate, 5–7 cm long, acute at apex, drying reddish brown (B & K yellow-red 04/05), persisting semi-intact at the upper nodes. *Leaves* erect-spreading; petioles 8–20(32) cm long, ca. 8 mm diam., D- to C-shaped, broadly to narrowly sulcate adaxially, with the margins blunt, rounded abaxially; geniculum 1–2 cm long; sheath to 6 cm long; blades coriaceous, elliptic to broadly elliptic or oblanceolate, acuminate at apex (the acumen to 2 cm long), occasionally obtuse at base, but mostly acute to decurrent, 40–112 cm long, (11)17–43 cm wide, broadest at or above the middle, the margins flat to broadly undulate; upper surface glossy, dark green, lower surface glossy to matte, paler, often sparsely to moderately pustulate or glandular; both surfaces drying yellowish green; midrib flat at base, becoming convexly raised toward the apex above, obtuse to acute-raised below; primary lateral veins 6–9 per side, departing midrib at 25–50° angle, mostly ascending, ± straight to the margin, sometimes loop-connecting in the uppermost portion of the blade, raised above and below; tertiary veins etched above, weakly raised below; collective vein arising from near the apex or absent, sunken above, raised below. *Inflorescences* erect; peduncle 36–95 cm long, 3–10 mm diam., 2–9× as long as petiole, olive-green, terete; spathe spreading-reflexed, recurled, subcoriaceous, green heavily tinged with maroon especially on the inner surface, with raphide cells, linear-lanceolate, 10–23 cm long, 1–2.5 cm wide, broadest near the base, acute at apex, decurrent at base; spadix dark red to dark violet-purple (B & K purple 2/7.5), sessile or stipitate to 10 mm, cylindroid to tapered, erect, 11–39 cm long, 6–7 mm diam. near base, 4 mm diam. near apex, broadest at the base or near the middle; flowers rhombic, ca. 2.4 mm long, ca. 1.4 mm wide, the sides straight; 7–9 flowers visible in principal spiral, 8–10 in alternate spiral; tepals matte, papillate; lateral tepals 1–1.4 mm wide, the inner margins ± straight to broadly convex, the outer margins 2–3-sided; pistils not emergent; stigma linear, 0.4–0.6 mm long, appearing granular; stamens emerging in a regular sequence from the base, the laterals preceding the alternates by 28 spirals, the 3rd stamen preceding the 4th by 6 spirals, inclined over and obscuring pistil;

anthers 0.4–0.6 mm long, 0.6–0.8 mm wide; thecae ovoid, slightly divaricate; pollen pale orange. *Infructescence* pendulous; spathe withered or absent; spadix 22–53 cm long, 1.4–1.7 cm diam., mostly bearing berries in the basal portion only; stipe to 10 cm long; immature berries reported as brown.

Anthurium pachylaminum is known from Loreto, San Martín, and Pasco in Peru at (240)320 to 770 m. It may be epiphytic or terrestrial in sandy, inundated soils and on steep slopes in tropical moist and premontane wet forest life zones.

This species is distinguished by its unusually large, coriaceous leaf blades (hence the name), with the tertiary veins etched into the upper surface (when fresh) and the primary lateral veins departing the midrib at an acute angle and running more or less straight to the margin. The leaf blades of *A. pachylaminum* are often pustular or glandular on the lower surface, and the spathe does not wither at anthesis, but often persists and remains in a weathered condition on the fruiting spadix.

Anthurium pachylaminum bears a similarity in leaf shape and inflorescence shape and color to *A. atropurpureum* var. *arenicola*. The latter, however, has mostly eglandular lower leaf surfaces, and the spathe withers at anthesis. It also generally has smaller leaves and shorter peduncles (1–4× as long as petiole) than *A. pachylaminum* (2–9× as long as petiole).

PERU. LORETO: Prov. Alto Amazonas, Río Capihuari, 5 km NE of Andoas, near Ecuador border, 240 m, *Gentry & Díaz 28226* (MO, NY); Prov. Maynas, Río Tacshacuraray, *Croat 20389* (F, MO, USM). PASCO: Prov. Oxapampa, Iscozazin–Villa America, Palcazú Valley, 300 m, 10°12′S, 75°13′W, *Smith 3855* (MO); Río Iscozazin, Cabeza de Mono, 10 km SW of Iscozazin, Palcazú Valley, 320 m, 10°20′S, 75°18′W, *Gentry et al. 41949* (MO). SAN MARTÍN: Moyobamba–Chachapoyas, Km 430–431, E of Naranjos at Río Naranjos, 770 m, 5°21′S, 77°20′W, *Croat 58161* (AAU, B, BM, CAS, F, G, GH, K, M, MO, NY, P, QCA, RSA, SEL, U, US, USM); Río Huallaga, Tocache Nuevo–Juanjui, 65.5 km S of Juanjui, 16 km S of Río Pulcache, 700 m, 7°50′S, 76°40′W, *Croat 58076* (MO); 65.5 km N of Tocache Nuevo, 114.5 km S of Juanjui, 16 km S of Río Pulcache and village of San Martín, 700 m, 7°50′S, 76°40.5′W, *Croat 58063* (MO); 56 km W of Rioja, 2 km E of Naranjos, 770 m, 5°51′S, 77°40′W, *Knapp et al. 7451* (BM, MO); Prov. Mariscal Cáceres, Dtto. Tocache Nuevo, Fundo de Las Flores, 550–600 m, 8°10′S, 76°33′W, *Croat 50990* (K, MO); Quebrada de Canuto, 500 m, *Schunke 10945* (CM, MO); Quebrada de Ishichimi, Tocache, 400 m, *Schunke 10047* (MO); Río Tocache, Puente Palo Blanco, 10 km W of Tocache Nuevo on rd. to Puerto Pizana, 550–650 m, 8°14′S, 76°36′W, *Plowman et al. 11347* (F); Puente Palo Blanco, 500–550 m, 8°14′S, 76°36′W, *Plowman & Schunke 7432* (F).

Anthurium palenquense Croat, sp. nov. TYPE: Ecuador. Los Ríos: Río Palenque Science Center, along trails W of laboratory and in vicinity of laboratory clearing, 210–250 m, *Croat 38670* (holotype, MO 2395515; isotypes, AAU, B, K, NY, QCA, PMA, RSA, US). Figures 221, 223, 224.

Planta terrestris; internodia brevia, 1–1.2 cm diam.; petiolus (6)10–30 cm longus, 5–20 mm latus, triangularis; lamina elliptica ad lanceolata ad oblanceolata, basi attenuata; nervis primariis lateralibus (9)14–30 utroque; pedunculus 10–60 cm longus, 2–10 mm latus, quadrangularis vel 2–4-costatus; spatha angusti lanceolata ad oblonga-lanceolata, 3–12 cm longa, 0.5–2.5 cm lata, viridis; stipes liber ad 1–5 mm; spadix contractus, (2)4–12 cm longus, 6–9 mm latus prope basim, 3–4 mm latus prope apicem, flavo-virens; baccae ovoideae, purpureae, 5–11 mm longae, 5–6 mm latae.

Terrestrial; stem green turning brown, calloused, 15–30 cm long, 1–2.5 cm diam.; leaf scars obscured by root mass, 1 cm high, 1–1.5 cm wide; roots numerous, descending, grayish or green, smooth or scurfy, blunt, 1–20 cm long, 2–5 mm diam.; cataphylls membranous to subcoriaceous, lanceolate, 4.5–17 cm long, narrowly acute and apiculate at apex, green tinged reddish at margins, drying pale tan (B & K yellow 5/10), persisting semi-intact or as coarse linear fibers or as bundles of linear fibers, often with the apex remaining intact. *Leaves* erect to spreading; petioles (6)10–30 cm long, 5–20 mm diam., sharply triangular, flattened to broadly convex adaxially, the margins winged, sharply angular abaxially; geniculum scarcely thicker and slightly paler than petiole, the angular ribs often conspicuously and minutely undulate, 1–3 cm long; sheath 1–2 cm long; blades subcoriaceous to coriaceous, elliptic to lanceolate or oblanceolate, long-acuminate at apex (the acumen flat to slightly inrolled), attenuate with conspicuously concave margins at base, (16)30–64(70) cm long, (7.5)10–23 cm wide, broadest usually near or below the middle, the margins broadly undulate; upper surface matte, velvety, the cells convex, sunken, forming an alveolate pattern when dried, dark green (B & K green 4/2.5), lower surface matte, paler (B & K green 7/2.5); midrib flat to obtusely angular at base, becoming sharply acutely raised toward the apex above, acutely raised (knife-edged), and higher than broad below; primary lateral veins (9)14–30 per side, departing midrib at 40–65(80)° angle, ascending straight to the collective vein, weakly sunken to weakly raised above, darker than surface and weakly raised below; interprimary veins numerous, scarcely sunken, ± parallel to and less conspicuous than primary

lateral veins; tertiary veins obscure above and below; collective vein arising from near the base, weakly sunken or weakly raised above, weakly raised or flat below, prominulous when dried, equally as prominent as primary lateral veins, 5–18 mm from margin. *Inflorescences* erect to slightly spreading or ± pendent, shorter than leaves; peduncle 10–60 cm long, 2–10 mm diam., 0.3–3× as long as petiole, green to dark purple or heavily tinged-mottled with red-purple (B & K red-purple 2/2.5), ± quadrangular or with 2–4 irregular ribs and convex sides; spathe spreading and weakly twisted or reflexed, membranous to subcoriaceous, green tinged maroon at margins and along main nerves (B & K red-purple 2/10), minutely pale-speckled (at least abaxially), narrowly lanceolate to oblong-lanceolate, 3–12 cm long, 0.5–2.5 cm wide, broadest near base, inserted at 30–90° angle on peduncle, acuminate at apex (the acumen inrolled, (2)5–15 mm long), acute to decurrent at base; stipe 3–15 mm long in front, 1–5 mm long in back; spadix yellow-green tinged with purple, becoming purple-violet or dark green tinged purplish at anthesis, cylindroid, sometimes weakly tapered, erect to curved, (2)4–12 cm long, 3–5 mm diam. near base, 3–4 mm diam. near apex; flowers with a faint, sweet, fruity scent, square to rhombic, 2–3.8 mm long, 1–3.8 mm wide, the sides straight to gradually sigmoid; 2–5 flowers visible in principal spiral, 2–6 in alternate spiral; tepals matte to semiglossy, minutely papillate and weakly punctate; lateral tepals 1.4–2.6 mm wide, the inner margins broadly convex, turned up against pistil, the outer margins 2-sided; pistils exserted 0.4–1.5 mm, glossy, green, sometimes tinged with purple around the stigma; stigma ellipsoid, greenish, 0.4–0.8 mm long, 0.25–0.4 mm wide, brushlike with blunt papillae, droplets appearing 1 week before stamens emerge; stamens emerging rapidly in a regular sequence from the base, the laterals preceding the alternates by 5–28 spirals (by ca. ¾ the length of the spadix), held erect above tepals and pistil; filaments translucent, exserted, 0.6–1 mm long, 0.4 mm wide; anthers orange (B & K yellow-red 7/10), 0.4–0.6 mm long, 0.5–0.7 mm wide, not obscuring pistil; thecae ellipsoid, 0.25 mm wide, weakly divaricate; pollen orange to yellow fading to cream-white (B & K yellow-red 7/2.5). *Infructescence* with spathe persisting; spadix 5–15 cm long, 0.5–1.5 cm diam.; berries dark purple, ovoid, acute at apex, 5–11 mm long, 5–6 mm diam.; pericarp thickened, with numerous raphide cells; seeds 1–2 per berry, with numerous raphide cells, rounded to ovoid, usually flattened on one side, 4–5.6 mm long, 3.2–3.8 mm diam., 1–2.8 mm thick, with a translucent gelatinous appendage at both ends.

A member of series *Multinervia*, *Anthurium palenquense* occurs in Ecuador in Esmeraldas, Cotopaxi, Los Ríos, and Pichincha provinces, at 80 to 400 m, typically in mature forest or in disturbed primary forest in tropical moist and premontane wet forest life zones. Most collections were made at the Río Palenque Biological Station in Los Ríos, hence the name.

Anthurium palenquense is distinguished by its terrestrial habit, coarse cataphyll fibers, triangular-winged petioles and closely veined, bicolorous blades which are attenuate at the base and matte to semi-velvety on the upper surface. In addition, the long-exserted stamens and the brushlike stigma are characteristic. An unusual feature is the pale raphide cells speckling the petioles, spathe, tepals, and even the filaments, as well as the pericarp and seed coat. This species (erroneously reported as *A. buenaventurae* Engl.) is pollinated by *Eulaema bomboides* (Dodson & Gentry, 1978).

Two collections of *Anthurium palenquense* from Esmeraldas and Cotopaxi (*Asplund 16306* and *Sparre 17214*), do not display the brushlike stigma (typical of the species), but agree in other characters with the present overall concept of *A. palenquense*.

Anthurium palenquense is most closely related to *A. napaeum*, which differs in having the leaf blades mostly acute at the base with convex to more or less straight (rather than concave) margins.

ECUADOR. COTOPAXI: Quevedo–Latacunga, 44.7 km E of Quevedo, 400 m, 0°51′S, 79°12′W, *Croat 55862* (AAU, CAS, DUKE, GB, JBGP, MO, OOM, QCA, RSA, SAR, TEX, US); Río Guapara, 20 km NW El Corazón, 250 m, *Sparre 17214, 17465, 17466* (S). ESMERALDAS: Quinindé, Rosa Zarate, *Asplund 16306* (S); Río Esmeraldas, Río Mutil, 6.6 km beyond Univ. Techn. Luis Vargas Torres–Est. Exp. Mutile, 80 m, 0°52′N, 79°33′W, *Croat 55610* (MO, QCA, U). LOS RÍOS: Quevedo–Santo Domingo de Los Colorados, Río Palenque Biological Station, 150–250 m, 0°35′S, 79°25′W, *Croat 38670* (AAU, B, K, MO, NY, QCA, PMA, RSA, US), *38688* (AAU, MBM, MO, NY, QCA, RSA), *49739* (MO), *50659* (CM, MICH, MO, SAR), *Dodson 5173* (MO, QCA, SEL, US), *Dodson & Gentry 12830* (SEL), *Dodson & McMahon 5059* (MO, SEL, US), *Gentry & Dodson 41298* (MO), *Lojtnant & Molau 15766* (AAU), *Madison 3742* (cult. at SEL) (MO), *Schupp 83* (SEL), *Watson 267* (NY). PICHINCHA: Santo Domingo–Quinindé, 300 m, *Solís 13952* (F).

Anthurium pallatangense Engl., Bot. Jahrb. Syst. 25: 385. 1898. TYPE: Ecuador. Cotopaxi: vic. Angamarca, *Sodiro s.n.* (holotype, B). Figures 222, 225.

Anthurium rumicifolium Sodiro, Anales Univ. Centr. Ecuador 15: 5. 1901. TYPE: Ecuador. Cotopaxi: Angamarca, 3,000 m, *Sodiro s.n.* (holotype, B).
Anthurium albopunctatum Sodiro, Anales Univ. Centr. Ecuador 22 (156): 22. 1906. TYPE: Ecuador. Pichincha: Nanegal, *Sodiro s.n.* (holotype, B).

Terrestrial or epiphytic; stem ca. 30–50 cm long, 1.5–2 cm diam.; leaf scars obscured by root mass, 0.5 cm high, 1 cm wide; roots dense, descending, greenish, drying tan to grayish, smooth to somewhat pubescent, slender and elongate, tapered at apex, ca. 4–26 cm long, 1–4 mm diam.; cataphylls lanceolate, 4–11 cm long, acuminate at apex, drying reddish brown, persisting as pale, fine, linear fibers. *Leaves* spreading-erect; petioles 10–33 cm long, 3–8 mm diam., terete to subterete, sometimes obtusely flattened adaxially, rounded abaxially; geniculum obscurely flattened, scarcely darker than petiole, 0.6–2 cm long; blades subcoriaceous, narrowly to broadly elliptic, occasionally oblanceolate, gradually acuminate at apex, slightly attenuate to narrowly acute to obtuse to subtruncate at base, 20–56 cm long, 4–15 cm wide, broadest at or near the middle; upper surface matte to semiglossy, dark to medium green, lower surface glossy to semiglossy, much paler; both surfaces drying matte to semiglossy, bright green to yellowish; midrib round-raised at base, becoming very narrowly and sharply raised (knife-like) toward the apex above, prominently and convexly raised with a sharp rib below; primary lateral veins 12–35 per side, departing midrib at 45–55° angle, ± straight to the collective vein, prominently and sharply raised above, flat to raised below, very sharply raised above when dried; interprimary veins drying almost as conspicuous as primary lateral veins, sharply raised above; tertiary veins obscure, drying prominulous; collective vein arising from the base, scarcely visible above, flat below, less prominent than primary lateral veins when dried, 3–11 mm from margin. *Inflorescences* spreading-erect, shorter than leaves; peduncle 6.2–29(38) cm long, 2–6 mm diam., (0.9)1.9–2.7× as long as petiole, pale green, tinged with violet-purple, subterete to angulate; spathe spreading to reflexed and recurled, subcoriaceous, green to green tinged with purple at margins and on veins, oblong-lanceolate, 2.5–7 cm long, 7–10 mm wide, broadest near the base, inserted at 65° angle on peduncle, acute to shortly acuminate at apex (the acumen apiculate), acute at base; stipe 7–10 mm long in front, 3–6 mm long in back; spadix maroon to purple, becoming brown (B & K red-purple 2/7.5), cylindroid, sometimes slightly tapered at apex, 3–8 cm long, 3–6 mm diam. midway; flowers 4-lobed, 2.1–2.4 mm in both directions, the sides jaggedly sigmoid; 3–5 flowers visible in principal spiral, 6–8 in alternate spiral; tepals matte, weakly papillate, with droplets; lateral tepals 1–1.3 mm wide, the inner margins straight to convex, slightly turned up against the pistil, the outer margins irregularly 3–4-sided; pistils raised, green; stigma ellipsoid; stamens emerging in a scattered pattern from the base of the spadix; filaments transparent, thick, exserted, soon retracting, holding anthers at level of the tepals, ca. 0.3 mm long, 0.4 mm wide; anthers yellowish heavily tinged with maroon, 0.6 mm long, 0.9 mm wide, inclined over and obscuring the pistil; thecae oblong, not divaricate; pollen orange, fading to tan. *Infructescence* with spathe persisting; spadix 6 cm long, 1.3 cm diam.; berries purple, obovoid, truncate at base, rounded and somewhat mammilliform at apex, 6–6.8 mm long, 3.7–4.5 mm diam.; seeds 2 per berry, brownish, oblong, flattened, rounded at both ends, 3.2–3.5 mm long, 2.2–2.5 mm diam., 1.5–1.7 mm thick, enveloped by gelatinous, translucent, amber substance.

A member of series *Multinervia*, *Anthurium pallatangense* is endemic to Ecuador in Carchí, Pichincha, Cotopaxi, and Chimborazo provinces at (1,710) 2,000 to 3,000 m. It occurs in lower montane dry, premontane dry, and montane moist forest life zones.

This species is distinguished by its broadly elliptic leaf blades with the primary lateral veins drying sharply raised (knife-edge-like) and a collective vein arising more or less from the base. In these characteristics it is very similar to *A. penningtonii*, probably its closest ally. Were it not for their geographical separation (either side of the Andes), *A. penningtonii* might be relegated to subspecific or varietal status. *Anthurium penningtonii* differs, however, in its green spadix (sometimes tinged purple or brown), and occurs in wetter life zones as well.

ECUADOR. CARCHÍ: 7.8 mi. SE of Maldonado, rd. to Tulcán, 2,400 m, 0°53′N, 78°5′W, *Thompson & Rawlins 888* (CM); Maldonado–Tulcán, Km 205, 2,400–2,600 m, *Werling & Leth-Nissen 362* (QCA). CHIMBORAZO: Pallatanga, *Sodiro 24* (B). COTOPAXI: Angamarca, ca. 3,000 m, *Sodiro s.n.* (B). PICHINCHA: Aloág-Santo Domingo, San Ignacio, 2,000 m, *Sparre 14687, 17742* (S); Machachi–Santo Domingo, 40.8 km E of Alluriquín, 2,050 m, 0°26′ S, 78°40′W, *Thompson & Rawlins 1094* (CM); Tandayapa–Mindo, 15.1 km beyond Tandayapa, 2,400 m, *Croat 49374* (MO, QCA); Nono–Nanegal, NW of Quito, 11–12 km NW of Nono, 2,200–2,270 m, *Croat 38837* (MO); Nanegal, *Sodiro s.n.* (B); Mindo-Tandayapa, 10 km SW of Tandayapa, 2,200 m, 0°00′N, 78°32′40″W, *Croat & Rodríguez 61545* (MO); Chiri-

boga Road, Chiriboga–Santo Domingo de Los Colorados, El Volante, 1,900 m, *Asplund 17418* (S); Quito–Santo Domingo de Los Colorados, 19 km S of San Juan, 15 km NE of Chiriboga, 1,710 m, 0°17′S, 78°43′W, *Croat 50621* (MO); Río Alambi, Nono–Tandayapa, km 43–45, 2,000–2,500 m, *Sparre 17016* (S); Quito–Puerto Quito, 13 km NW of Nono, 2,225 m, *Luteyn & Lebrón-Luteyn 6523* (NY); Volcán Pichincha, W side, Tandayapa–Mindo, 2,300 m, 0°2′S, 78°42′W, *Croat 50256* (MO, RSA, USM).

Anthurium paraguayense Engl., Bot. Jahrb. Syst. 25: 361. 1898.

a. Anthurium paraguayense var. **paraguayense**. TYPE: Paraguay. Central: Asunción, Colonia Elisa, *Lindman A1823* (holotype, B; isotype, S). Figures 226, 227, 231.

Anthurium rodrigoi A. Hawkes, Phytologia 3: 27. 1948. TYPE: Argentina. Chaco: Tapenaga, Enrique Urien, *Rodrigo 2690* (holotype, NY).

Anthurium rusticum N. E. Br. ex Engl., Pflanzenr. IV. 23B(Heft 21): 82. 1905. TYPE: Bolivia. La Paz: Yungas, Coroico, *Bang 2479* (holotype, NY; isotypes, GH, MO).

Terrestrial or epiphytic; stem to 40 cm long, (1)5–6 cm diam.; roots numerous, dense, descending or ascending, green or tan, smooth to pubescent, blunt, longitudinally fissured when dried, 3–10 cm long, 2–5 mm diam.; cataphylls membranous to subcoriaceous, 3–9.5 cm long, acute and sharply 1-ribbed at apex (apiculate to 1 mm), pale green, drying dark brown to tan (B & K yellow 6/5), persisting as a reticulum of fibers at base. *Leaves* erect to spreading; petioles 3–28.5 cm long, 6–10 mm diam., D-shaped to sometimes nearly quadrangular, shallowly sulcate with a medial rib adaxially, the margins acutely raised, bluntly to sharply 1–3-ribbed abaxially, the surface green sometimes pale-speckled; geniculum thicker and paler than petiole, 0.7–2.5 cm long; sheath 0.9–2.5 cm long; blades subcoriaceous, oblanceolate to oblong-oblanceolate, long-acuminate at apex (the acumen inrolled to flat), acute to obtuse to rounded or truncate at base, 22–100 cm long, 5–19.5 cm wide, broadest above the middle, the margins prominently undulate; both surfaces semiglossy to matte, dark to medium green above, paler or concolorous below; both surfaces drying usually greenish; midrib broadly raised at base with an acute medial rib, diminishing and becoming sunken toward the apex above, slightly raised when dried, convexly raised at base, becoming acute and then narrowly raised toward the apex above, slightly raised when dried; primary lateral veins 4–10 per side, departing midrib at (25)30–70° angle, arcuate-ascending to the margin or loop-connecting to the primary lateral vein above it, raised above near the midrib, weakly sunken at the margin, raised below; interprimary veins obscure above, visible below; collective vein arising from near the apex, weakly sunken above, bluntly raised below, prominulous when dried, 5–9 mm from margin. *Inflorescences* erect or spreading, shorter than leaves; peduncle 14–65 cm long, 8–9 mm diam., ca. 2–6× as long as petiole, dark green, terete to subterete; spathe spreading to reflexed with the margins rolled under, coriaceous, dark green tinged with purple (B & K yellow-green 4/7.5), lanceolate to ovate-lanceolate, (2)6–15 cm long, (0.7)1.7–3 cm wide, broadest in the lower third, inserted at 40–50° angle on peduncle, acute to acuminate at apex (the acumen inrolled), acute to decurrent at base, minutely verruculose on inner surface; spadix green tinged with purple or gray-brown (B & K yellow 5/7.5), tapered, (2.4)5–15 cm long, 4–15 mm diam. near base, ca. 3–8 mm diam. near apex; flowers 4-lobed to rhombic, (1.7)2.5–4 mm long, (2.2)2–4 mm wide, the sides jaggedly sigmoid; 5–8 flowers visible in principal spiral, 7–10 in alternate spiral; tepals matte, sometimes appearing punctate and papillate; lateral tepals 0.9–1.5 mm wide, the inner margins convex or straight, the outer margins smoothly 3–4-sided; pistils not emergent or scarcely emergent, green tinged with purple; stigma ellipsoid to slit-like, 0.2–0.5 mm long; stamens emerging in a regular sequence, emerging shortly above the tepals, the laterals preceding the alternates by 10–12(21) spirals, the 3rd stamen preceding the 4th by 3–4 spirals; filaments translucent, with raphides, 1–1.5 mm long; anthers yellowish to red-purple (B & K red-purple 7/5), 0.5–0.7 mm long, 0.8–0.9 mm wide, inclined over and obscuring the pistil; thecae oblong-obovoid to oblong-ellipsoid, slightly or not at all divaricate; pollen pale yellow to cream, scented like grass. *Infructescence* spreading-pendent; spathe persisting; spadix 17.5–20 cm long, to 3.5 cm diam.; berries reddish to maroon (B & K red-purple 2/7.5), obovoid, rounded at apex, 5–10 mm long, 3–6 mm diam.; pericarp moderately thickened, with raphide cells at base; mesocarp translucent to milky, thick-gelatinous; seeds 2 per berry, white, streaked with reddish or maroon, ovoid, flattened, 5–6.2 mm long, 2.5–3.4 mm diam., 1–2 mm thick, with a gelatinous appendage at both ends.

Anthurium paraguayense is a common terrestrial, occasionally epiphytic species of southern Brazil (Mato Grosso Sul), Bolivia, Paraguay, and northern Argentina. It is mostly reported from dry

areas, on steep slopes and sandy or rocky soils at 150 to 1,700 m. In Bolivia it occurs in subtropical moist and lower montane subtropical wet forest life zones.

This species is distinguished by its long, narrow blade with undulate margins and by its petiole that is bluntly 1–3-ribbed abaxially and shallowly sulcate adaxially, with a prominent medial rib. Also characteristic is the peduncle, which is usually 2–6 times longer than the petiole, and its persistent, coriaceous spathe, which is verruculose on the inner surface, appearing to have minute grains of sand spread across it. Other diagnostic features include the presence of raphides in both vegetative and floral structures (including the blade, petiole, peduncle, spathe, filaments, tepals, berry, and seed coats).

Anthurium paraguayense var. *paraguayense* is similar to var. *coroicoanum*, with which it may occur, but has a proportionally longer peduncle compared to the petiole, and a persistent spathe that appears rather verruculose adaxially. Both taxa are represented by an unusually high proportion of fruiting specimens in herbaria. The var. *coroicoanum* is distinguished by its broadly elliptic leaf blades with reflexed basal primary lateral veins, while var. *paraguayense* has lanceolate to oblanceolate blades lacking any reflexed venation. The two taxa occur in similar habitats and elevations in close geographic proximity.

A noteworthy collection is *Beck 6996*, from the Department of Beni, Bolivia, which has the lowermost primary lateral veins spreading at a ca. 90° angle from the midrib, but otherwise demonstrates all the characteristics of the typical variety.

ARGENTINA. CHACO: Tapenanga, Enrique Urien, *Rodrigo 2690* (NY); General Vedia, *Meyer 2406* (GH). CORRIENTES: Dpt. San Ignacio, San Ignacio, *Schinini 20961* (K, MO); Dpt. San Luis del Palmar, 65 km SE of San Luis del Palmar, Ruta 5, *Schinini et al. 21647* (K). FORMOSA: *Jorgensen 2349* (MO), *2347* (GH, US); Dpto. Pilcomayo, Parque Nacional Pilcomayo, *Charpin & Eskuche AC 20316* (MO, US). BOLIVIA. WITHOUT LOCALITY: *Bang 1660* (F), *2581* (NY); *Rusby 2479* (F, NY, US). BENI: Prov. Ballivian, Río Yacuma, Espíritu, 200 m, *Beck 3296* (B, K, MO, TEX); Serranía de Pilón Lajas, 75 km from La Paz, San Borja, 950 m, *Beck 6996* (MO). LA PAZ: Canamina, 1,500 m, *Rusby 375* (NY); Prov. Larecaja, Caranavi–Guanay, 27.8 km N of Caranavi, 865 m, 15°33′S, 67°45′W, *Croat 51646A* (MO); Prov. Loayza, Chulumani–Circuata, Km 9, Miquilla, 1,530 m, *Besse et al. 1852* (SEL), *Christenson 1533* (MO); Prov. Morillo, Valle de Zongo, along trail from end of rd. at Kahua Power Plant, 1,660–1,690 m, *Croat 51406* (MO); Prov. Nor Yungas, Coroico, *Bang 2479* (GH, MO, NY); Coroico, Polo-Polo, 1,100 m, *Buchtien 3654, 4516* (US); Millaguaya, 1,300 m, *Buchtien 4284* (NY, US); Chuspipata–Yolosa, 20 km NE of Chuspipata, 10.2 km SW of Yolosa, 1,700 m, 16°12′S, 67°47′W, *Solomon & Uehling 12252* (MO); Unduavi–Caranavi, 82.6 km NE of Unduavi, 1,300 m, *Croat 51559* (MO); Río Huarinilla, 4.5 km below Yolosa, then 10 km W on rd. up Río Huarinilla, 1,450 m, 16°12′S, 67°50′W, *Solomon 8560* (MO); Prov. Sud Yungas, 22 km toward new bridge on Río La Paz, Irupana, 1,100 m, *Beck 2962* (MO). SANTA CRUZ: Concepción–San Javier, *Evrard 8483* (BR); Chavez, El Carmen, 40 km S of Concepción on road to Lomerio, 750 m, *Killeen 1447* (MO); Río Ichilo, Valle Grande, Vallecito, 1,300 m, *Cárdenas 4006* (US). BRAZIL. MATO GROSSO SUL: near Bela Vista on road to Caracol, *Hatschbach & Silva 51585* (MBM, MO). PARAGUAY. WITHOUT LOCALITY: *Palmer s.n.* (US); Cerro San Bernardino, *Chodat 345* (G); Cordillera de Los Altos, *Fiebrig 348* (G, MO), *Hassler 1170, 1503, 3264* (G); Cerro de Tabati, *Schinini 21254* (CTES); Co. de Caacupe, *Schinini 23882* (CTES). AMAMBAY: Parque Nacional Cerro Cora, *Schinini & Bordas 20315* (CTES, K); Cerro Muralla, 1.5 km N of administración, *Brunner et al. 977* (MO); 7 km SW of administración, paso Nandejara, 250–300 m, *Simonis et al. 132* (U); Cerro Muralla, 300–350 m, 22°39′S, 56°03′W, *Casas & Molero 3960* (NY), *6061* (G, MO), *Solomon et al. 6782* (MO), *Zardini et al. 4120* (MO, PY); peñasco Guaiguy Hog, *Casas & Molero 4045* (NY); Río Aquidaban Nigui, Sierra de Amambay, *Hassler 11157* (G). ASUNCIÓN: Colonia Independencia, *Schinini 5644* (CTES), *Schinini & Bordas 21238, 21234, 21235* (CTES); Río Paraguay, *Balansa 578* (K). CAAZAPÁ: Río Tebicuari, *Kuntz 1492* (NY). CENTRAL: Asunción, Colonia Elisa, *Lindman 1823* (B); Río Paraguay, Villa Elisa, *Pedersen 58* (BR), *3150* (GH, US); Cerro Yaguaron, Yaguaron, *Arenas 953* (CTES). CORDILLERA: Caacupe, 25°20′S, 57°10′W, *Hahn 2028* (MO); Cerro Tabatí, *Zardini & Degen 3688* (MO, PY), *3692* (G, MO, PY); Serranía de Tobatí, Meseta Ybytú Silla, 297 m, 25°12′S, 57°07′W, *Zardini 8283* (CTES, FCQ, G, MO); Colonia Rosado, Tobatí, 200 m, 25°16′S, 57°07′W, *Schinini & Bordas 24882* (CTES). ÑEEMBUCÚ: Pilar, *Schulz 7865* (CTES). PARAGUARÍ: Cerro Acahay, 25°54′S, 57°9′W, 370 m, *Brunner 1249* (MO); Acahay, *Chodat 346* (G); Parque Nacional Ybycuí, *Duré 414* (MO). PRESIDENTE HAYES: Estancia La Golondrina, Villa Hayes, 24°55′S, 57°40′W, *Hahn 698* (MO); Trans-Chaco Hwy., Km 127, 150 m, *Gentry et al. 51990* (MO). SAN PEDRO: Río Apa-Aquidabán, Alto Paraguay, *Fiebrig 4149* (G, K); Río Tapiracuai, Alto Paraguay, 20–28°N, 59–63°W, *Woolston 1074* (K, NY, U, US); Dtto. Lima, Jejui, Estancia "Carumbe," *Pederson 9417* (K).

b. Anthurium paraguayense var. **coroicoanum** Croat, var. nov. TYPE: Bolivia. La Paz: between Caranavi and Guanay, 28.1 km N of Caranavi, near bridge over Río Coroico, 15°27′S, 67°50′W, 820 m, *Croat 51704* (holotype, MO 2825694; isotypes, B, K). Figures 228, 229, 232.

Differt a var. typicum per laminum ellipticum, nervis primarii lateralis reflexis.

Terrestrial to epiphytic; stem to 20 cm long, 1–4 cm diam.; roots dense, greenish, pubescent, short, thick and blunt at apex, 2–5 cm long, 4–5 mm

diam.; cataphylls subcoriaceous, lanceolate, unribbed, 2.5–10 cm long, acute at apex, green (B & K yellow-green 9/2.5), drying dark to medium brown (B & K yellow 3/2.5), persisting semi-intact, eventually as coarse linear fibers or as a reticulum of fibers. *Leaves* erect to spreading; petioles 5.5–26 cm long, 4–5 mm diam., D-shaped to C-shaped, flattened with blunt to sharp margins adaxially, sometimes with a medial rib, rounded abaxially; geniculum paler than petiole, up to 11 cm remote from the base of the blade, 0.6–1 cm long; blades subcoriaceous, elliptic to ovate-elliptic, acute at apex, acute to prominently attenuate at base, 24–43 cm long, 8–25 cm wide, broadest at or near the middle, the margins broadly undulate; upper surface semiglossy to glossy, lower surface weakly glossy to semiglossy, both drying matte, brownish to brownish green; midrib sharply and acutely raised above, conspicuously paler than surface, convexly to obtusely raised at base below, becoming flat toward the apex, paler than surface; primary lateral veins 4–9 per side, departing midrib at 55–85° angle, weakly arcuate in the middle of the blade, ± reflexed at base, prominently raised above, raised below; interprimary veins weakly visible; tertiary veins visible; reticulate veins obscure; collective vein arising from about the middle of the blade, flat above and below, slightly darker than surface below, 1–7 mm from margin. *Inflorescences* erect-spreading, shorter than leaves; peduncle 12.5–26 cm long, 4 mm diam. when fresh, 1–2 mm diam. when dried, 0.8–3.8× as long as petiole, green (B & K yellow-green 8/7.5), terete; spathe reflexed to recurled, subcoriaceous,medium green, sometimes tinged with purple at margins (B & K yellow-green 6/7.5), lanceolate, 3–5 cm long, 0.8–2 cm wide, broadest near the base, inserted at 30–60° angle on peduncle, acute to short-acuminate at apex (the acumen inrolled, ca. 2 mm long), acute at base, the margins meeting at 45° angle; spadix greenish tinged with reddish to pale pink, also reported as becoming purplish post anthesis, long-tapered to nearly cylindroid, erect, 4.5–6.5 cm long, 4–8 mm diam. near base, 3–5 mm diam. near apex, broadest at the base; flowers rhombic to 4-lobed, 1.6–2.5 mm long, 1.8–2.2 mm wide, the sides jaggedly sigmoid; 7–9 flowers visible in principal spiral, (6)14–15 in alternate spiral; tepals semiglossy to matte, with droplets; lateral tepals 1–1.2 mm wide, the inner margins straight to convex, the outer margins usually 2-sided (meeting at ca. 90° angle), occasionally 3–4-sided; pistils weakly exserted, dark brownish purple; stigma slit-like, 0.5–0.6 mm long; stamens emerging rapidly in a regular sequence from the base, held shortly above the tepals, the laterals preceding the alternates by 13–14 spirals, the 3rd stamen preceding the 4th by ca. 2 spirals; anthers orange to reddish purple, 0.4–0.5 mm long, 0.6–0.8 mm wide, inclined over and obscuring the pistil; thecae oblong, 0.3–0.4 mm wide; pollen yellow fading to white, weakly fruity-scented. *Infructescence* with purple berries.

Anthurium paraguayense var. *coroicoanum* is known only from the vicinity of the type locality in La Paz Department, Bolivia, at 700 to 900 m in subtropical moist and subtropical wet forest life zones, and from Cusco, Peru, at 800 m in a subtropical rainforest life zone.

Anthurium paraguayense var. *coroicoanum* differs from the typical variety in its more or less elliptic rather than oblanceolate leaf blades, and by having the lowermost primary lateral veins directed at an almost 90° angle from the midrib to prominently reflexed, vs. prominently ascending in the typical variety. Another character distinguishing the two taxa is berry color: purple in var. *coroicoanum*, dark red in var. *paraguayense*.

The new variety is named for the type locality, near the Río Coroico.

BOLIVIA. LA PAZ: Caranavi–Guanay, 27.8–28.1 km N of Caranavi, near bridge over Río Coroico, 820–865 m, 15°27–33′S, 67°45–50′W, *Croat 51657* (MO), *51704* (B, K, MO, NY). SANTA CRUZ: Prov. Ichilo, Parque Nacional Amboro, 15 km SE up the Río Pitasama from Río Surutú, 700 m, 17°44′S 63°40′W, *Solomon & Urcullo 14159* (MO). PERU. CUZCO: Prov. Paucartambo, Río Tono, N of Patria, Cosnipata Valley, 800 m, 13°07′S, 71°12′W, *Wachter et al. 141* (F, MO).

Anthurium pendulifolium N. E. Br., Gard. Chron. 36: 362. 1904. TYPE: unknown locality, possibly Colombia, *Kew H 457/83* (holotype, K). Figures 9, 230, 233, 234, 255.

Epiphytic, rarely terrestrial; stem pendent, 20–30 cm long, 1.5–3.5 cm diam.; leaf scars reported as conspicuous, ca. 2.8 cm wide; roots moderately dense, descending, brown, 6 mm diam.; cataphylls moderately coriaceous, broadly lanceolate, scarcely 1-ribbed, 4–19 cm long, acuminate at apex with subapical apiculum, green, drying brown (B & K yellow-red 9/2.5), persisting as coarse linear fibers, the apex remaining intact. *Leaves* spreading-pendent to pendent; petioles 27–65 cm long, 5–10 mm diam., terete to subterete or thicker than broad, slightly flattened adaxially, rounded abaxially, the surface minutely pale-speckled; geniculum paler and thicker than petiole, 1.5–3.5 cm long; sheath 2.5–12 cm; blades coriaceous to subcoriaceous, oblong to oblanceolate, acuminate at apex, acute

to rounded (rarely subcordate) at base, 64–190(207) cm long, 16–32(42.5) cm wide, broadest above the middle, the margins weakly revolute, broadly and weakly undulate; upper surface glossy to semiglossy, light to medium green (B & K yellow-green 5/10), lower surface matte, paler; midrib convexly to obtusely raised, paler than surface above, obtusely angled below; primary lateral veins (8)11–15 per side, departing midrib at 45° angle, arcuate-ascending to the margin, sunken in shallow grooves above, paler than surface, raised below; interprimary veins few, obscure; tertiary veins obscure above, scarcely raised and darker than surface below; collective vein arising in the lower third to about the middle of the blade, less prominent than primary lateral veins, (4)7–14 mm from margin. *Inflorescences* erect-spreading; peduncle 35–52 cm long, 0.5–1 cm diam., 0.5–1.7× as long as petiole, terete; spathe reflexed and twisted, subcoriaceous, pale yellowish green to creamy white, violet at margins and at base (B & K yellow-red 9/10), oblong-lanceolate, (9)20–30(60) cm long, 1.5–4.8 cm wide, broadest just above the base, acuminate at apex (the acumen inrolled), acute at base; stipe 8–12 mm long in front, 2–5 mm long in back; spadix reddish violet to reddish purple (B & K purple 2/7.5 to red-purple 7/5–10), tapered, curved, 19.5–38 cm long, 4–9 mm diam. midway, 2–4 mm diam. near apex; flowers weakly 4-lobed to rhombic, 2.5–3.5 mm long, 1.7–3.3 mm wide, the sides straight to sigmoid; 12–16 flowers visible in principal spiral, 8–27 in alternate spiral; tepals matte and weakly punctate; lateral tepals 1.4–2.2 mm wide, the inner margins broadly rounded to somewhat concave, the outer margins 3–5-sided; pistils glossy, weakly exserted, green; stigma brush-like; stamens emerging irregularly; filaments fleshy, translucent, minutely papillate, exserted 0.5 mm; anthers creamy white to yellow, 0.5 mm long, 0.6–0.7 mm wide, inclined over the pistil; thecae ovoid-ellipsoid to pyriform, weakly divaricate; pollen yellow fading to white. *Infructescence* pendent to spreading-pendent, sometimes coiled; spathe withered; spadix 27–55 cm long, 1–2 cm diam., with berries scattered throughout; berries lavender, becoming white at maturity, obovoid-oblong, rounded at apex, 10–11 mm long, 5–6 mm diam.; pericarp thickened; mesocarp mealy, white; seeds 1–2 per berry, brown, oblong, (5.5)7.3–7.8 mm long, 2.8–3 mm diam., 1.3 mm thick.

Anthurium pendulifolium ranges from Colombia (Amazonas and Putumayo) to northern Peru as an epiphyte at 90–550 m in tropical moist and tropical wet forest. Most collections are from the upper Río Napo and Río Aguarico in northern Ecuador (Napo), and also from around Iquitos in Loreto, Peru. It has also been collected in northern Amazonas, in Peru along the Río Cenepa and the Río Santiago, as well as along the lower Río Pastaza in northwestern Loreto. It is to be expected throughout lowland Ecuador and northwestern Loreto in Peru.

This species is distinguished by its oblong-oblanceolate leaf blades which are pendulous and dry pale green or yellowish green (the type specimen, of cultivated origin, has pale brown leaves, but this may be due to its age of nearly 100 years). Also distinctive are the moderately long petioles (up to ½ as long as the blades) and pale purple berries which become whitish in age. *Anthurium pendulifolium* may be confused with *A. atropurpureum* var. *arenicola*, with leaves drying the same green color and occurring in the same area. The latter differs from *A. pendulifolium* in its erect-spreading, rosulate habit, broadly oblanceolate leaf blades, shorter petioles, and conspicuously sunken tertiary veins (when fresh).

Anthurium pendulifolium was originally described from cultivated material thought to be from Colombia. While no Colombian material closely matches the type, much of the material collected in Ecuador matches it well.

Common names for this species include "yakiya sugkip" (Huambisa tribe, Río Santiago, Amazonas, Peru); "kankur nuka" (Río Santiago); "meko uko" (Siona Indians, Putumayo, Colombia); "fam'be" (Río San Miguel, Putumayo, Colombia); and "bagre panga" (Río Lagartacocha, Napo, Ecuador). The mashed, cooked leaves are used in a water bath by the Siona Indians (Putumayo, Colombia) to relieve bone aches and rheumatism.

WITHOUT LOCALITY: cultivated at Kew, *Kew H 457/83* (K). COLOMBIA. AMAZONAS: Puerto Nariño, Parque Nacional Amacayacu, 100 m, 3°45′S, 70°15′W, *Vásquez et al. 12506* (MO). PUTUMAYO: Buena Vista, *Piaguaje 28* (ECON); Río San Miguel, Santa Rosa de Sucumbios, 380 m, *Schultes 3609* (GH). ECUADOR. NAPO: Laguna Grande, Pica Saladero de Dantas, Cuyabeno, 0°00′00″, 76°12′45″W, *Jaramillo 6852* (MO, QCA); 265 m, *Nielsen 76272* (AAU, MO); Lago Agrio–Coca, 26 km N of Coca, 450 m, 0°29′S, 76°55′W, *Croat 50420* (MO); Coca–Hollín, Huaticocha, 500 m, 0°45′S, 77°29′W, *Palacios et al. 3543* (MO); Payamino, Reserva Floristica "El Chuncho," 250 m, 0°0′S, 77°01′W, *Cerón & Palacios 3000* (MO, QCNE); ridge W of Cotapino, parallel to Río Cotapino, 360 m, 0°40′S, 77°20′W, *Whitmore 718* (K); trail to Shushufindi, WSW of San Pablo de Las Secoyas, 300 m, 0°15′S, 76°21′W, *Brandbyge & Asanza 32892* (AAU, MO); Lago Agrio–Puerto El Carmen de Putumayo, 15 km E of Tarapoa, 91.7 km E of Lago Agrio, 260 m, 0°08′N, 76°23′W, *Croat 58579* (MO, QCA); 28 km W of Tarapoa, 48 km E of Lago Agrio,

240 m, 0°06′N, 76°33′W, *Croat 58610* (BM, MO, QCA, US, W); rd. to Agua Pungo, Tena, 1.5 km past bridge over Río Mishahuallí, 550 m, 0°59′S, 77°47′W, *Croat 58825* (MO); Estación Biológica Jatún Sacha, 8 km E of Mishahuallí, 450 m, *Palacios 2863* (MO); Parque Nacional Yasuní, 200 m, 0°55′S, 76°11′W, *Cerón & Hurtado 4012* (MO); Cantón Aguarico, lagunas de Garza Cocha, 200 m, *Cerón & Gallo 4953* (MO, QCNE); Cantón Tena, headwaters of Río Huambuno, 6 km NNW of Ahuano, 440 m, 1°00′S, 77°40′W, *Kohn 1155* (MO); Río Aguarico, E of Lago Agrio, road to Cepe Ferry Crossing, 450 m, 0°02′N, 76°50′W, *Croat 50427* (MO), *58513* (MO, P, QCA); Santa Cecilia, 200 m, 0°04′N, 76°58′W, *Sparre 13043* (S); Río Lagartococha, Redondo Cocha, 190 m, 0°35′S, 75°15′W, *Lawesson et al. 44424* (AAU). PASTAZA: Río Curaray, Lagunas Patoamo, 230 m, 1°30′S, 76°30′W, *Palacios & Neill 762* (MO, NY, QAME). PERU. AMAZONAS: Río Cenepa, *Croat 57196* (MO); Río Santiago, La Poza, 400 m (180 m), *Huashikat 150* (MO); Río Santiago, Quebrada Caterpiza, 2–3 km behind community of Caterpiza, 200 m, 3°50′S, 77°40′W, *Tunqui 784* (MO). LORETO: vic. Yanamono, Explorama Camp, 130 m, 3°28′S, 72°50′W, *Croat 61760* (AMAZ, MO), *66057* (MO); Prov. Alto Amazonas, Río Pastaza, Uchpayaco–Rimachi, 4°20′S, 76°40′W, *Díaz et al. 1287* (MO); Prov. Loreto, Pucayacu, native community of Shimaco–Urarina, *Vásquez 6033* (MO); Prov. Maynas, Iquitos Region, Río Itaya, 10 km above Iquitos, *Croat 19151* (MO); Quebrada de Bo, ca. 90 m, *Rimachi 6490* (IBE); Río Manití, Recreo, NE of Iquitos, 115 m, 3°42′S, 72°50′W, *Vásquez & Jaramillo 1123* (MO); Río Momón, tributary of Río Nanay, Iquitos, *Davidson & Jones 9802* (LAM); Sucusari, 116 m, 72°55′W, 3°20′S, *Vásquez & Jaramillo 8247* (MO); 11 km from Río Nanay, near Iquitos, Quebrada Momoncillo, 200 m, 3°43′S, 73°20′W, *Croat 51224* (COL, F, GH, M, MBM, MO, NY, SEL, U), *Davidson & Jones 9517* (LAM); Río Amazonas, Quebrada Panguanillo, Aucayo, 90 m, *Rimachi 6041* (IBE); Río Tacshacuraray, tributary of Río Napo, 2°40′S, 73°30′–74°20′W, *Croat 20380* (MO). SAN MARTÍN: Tarapoto–Yurimaguas, Km 54, Lamas, 350 m, 6°23′S, 76°18′W, *Knapp 8262* (MO).

Anthurium penningtonii Croat, sp. nov. TYPE: Ecuador. Napo: between Quito & Baeza, S of road above jct. of road to Baeza & to Lago Agrio, 1,800 m, *Croat 58491* (holotype, MO 3183150; isotypes, QCA, VEN, RSA, K, US). Figures 235, 236, 256, 257.

Planta terrestris aut raro epiphytica; internodia brevia, 1–3 cm diam.; cataphyllum lanceolatum, persistens semi-intactum mox fibris stramineis findens; petiolus 11–31 cm longus, 4–8 mm diam., subteres ad triangularis; lamina late elliptica, raro oblanceolata, 35–61 cm longa, 10–19 cm lata; nervis primariis lateralibus 24–43 utroque, acute elevatis; pedunculus 21–52 cm longus, 3–4 mm diam.; spadix viridis, 2.5–5.5 cm longus, 3–5 mm diam.

Terrestrial, rarely epiphytic; stem to 50 cm long, 1–3 cm diam.; roots dense, drying whitish to tan, moderately elongate; cataphylls thin, lanceolate, 6–13 cm long, acuminate at apex, drying reddish brown, persisting semi-intact, quickly weathering to straw-colored fibers. *Leaves* erect-spreading; petioles 11–31 cm long, 4–8 mm diam., subterete to triangular, flattened to broadly convex adaxially, sometimes with the margins sharp, rounded or sharply 1-ribbed abaxially; geniculum slightly paler and scarcely thicker than petiole, (0.6)1–3 cm long; sheath 1.5–3 cm long; blades coriaceous to subcoriaceous, broadly elliptic, rarely somewhat oblanceolate, shortly acuminate at apex, acute to narrowly acute at base, 35–61 cm long, 10–19 cm wide, broadest near the middle, the margins flat to slightly revolute; upper surface weakly glossy to semiglossy to glossy, dark to medium green, lower surface semiglossy, conspicuously paler; midrib convexly raised at base, becoming sharply acute toward the apex above, slightly paler than surface, acutely raised below; primary lateral veins 24–43 per side, departing midrib at 40–60° angle, straight to the collective vein, usually prominently and sharply raised above, flat to sunken below; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins obscure, prominulous above and below on drying; reticulate veins not visible; collective vein arising from the base, equally as prominent as primary lateral veins, 10–15 mm from margin. *Inflorescences* erect; peduncle 21–52 cm long, 3–4 mm diam., 1–2.2× as long as petiole, green to purple, terete, sometimes with many weakly to prominently raised striations; spathe reflexed or rarely spreading, subcoriaceous, green, usually tinged with purple, oblong-lanceolate, 3.5–7 cm long, 0.6–1.3 cm wide, broadest near the base, acute to abruptly acuminate at apex, acute at base; spadix green, usually tinged with purple to purplish brown, sessile or stipitate to 2 mm, scarcely tapered, erect, 2.5–5.5 cm long, 3–5 mm diam. midway, 3–4 mm diam. near apex; flowers square to rhombic, 1.4–2 mm long, 1.4–1.8 mm wide, the sides straight; 5–9 flowers visible in principal spiral, 4–6 in alternate spiral; tepals matte, minutely papillate; lateral tepals 1.1–1.2 mm wide, the inner margins rounded, the outer margins 2-sided; pistils emergent, glossy; stamens exserted; anthers pink-orange, 0.4–0.5 mm long, 0.5 mm wide; thecae oblong-ellipsoid, slightly divaricate; pollen pale orange fading to white. *Infructescence* erect; spathe persisting; spadix 8–10 cm long, 1.3–1.7 cm diam., with berries scattered throughout; berries (immature) green, emergent ca. halfway, obovoid, shortly beaked at apex on drying, ca. 6.5 mm long, ca. 4 mm diam.; pericarp with raphide cells; seeds 2 per berry, oblong-obovoid, flattened, beaked at apex, 4–4.5 mm long, 2.5–2.7 mm wide, 1.5–1.8 mm thick, with a gelatinous appendage at one end.

A member of series *Multinervia*, *Anthurium penningtonii* ranges from the Amazon slopes of Ecuador to northern Peru on both slopes of the Cordillera Oriental and the Cordillera Central at elevations of (800)1,000 to 2,500 m. The species is ecologically variable. In Ecuador it is known from premontane moist, premontane wet, lower montane moist, and lower montane wet forest life zones, while in Peru it is known from premontane rain and montane rain forest life zones.

This species is distinguished by its broadly elliptic, green-drying leaf blades with sharply raised (knife-edge) major veins, and by its rather remote collective vein (1–1.5 cm from the margin).

Anthurium penningtonii is not confused with any other species on the eastern side of the Andes, but *A. pallatangense*, from the Pacific slope of Ecuador, is very similar, differing mainly in its dark purple to maroon spadix. It occurs in drier life zones as well.

Some material from Morona–Santiago (*Stein 2826*, *Madison et al. 3457*, *Madison 2605*) has sharply triangular petioles. Considering the variation in the vicinity of Baeza alone (petioles terete to flattened adaxially and sometimes sharply 1-ribbed abaxially, sometimes with the margin sharp on one side), these collections are best placed in *A. penningtonii* and agree well in other characters. Another collection from Morona–Santiago (*Steyermark 53610*) differs in having the leaf blades attenuate at the base, rather than acute to narrowly acute. More collections from southern Ecuador and northern Peru are needed to determine the range of variability in this taxon.

The new species is named in honor of T. D. Pennington, a member of the 1960 Oxford University expedition to Ecuador and one of the first collectors of this species.

ECUADOR. MORONA–SANTIAGO: Limón (General Plaza)–Macas, 8 km N of Limon, 1,100 m, 2°57′S, 78°25′W, *Stein 2826* (B, K, MO, QCNE, US); 7–8 km N of Gualaquiza on road to Indanza, 1,450 m, *Harling & Andersson 24199* (GB, MO); Tumbez–Tucumbatz, Km 20 on road Gualaquiza–Indanza, 1,600 m, *Harling & Andersson 24360* (GB); Cordillera de Cutucu, Rio Chihuasi, 25 km SE of Lagrono, 800–1,000 m, *Madison 2605* (SEL); Lagrono–Yaupi, 1,600 m, 2°46′S, 78°06′W, *Madison et al. 3457*, *3502* (SEL); Río Tintas, Campanas–Arenillas, 10 leagues SE of El Pan, 2,195 m, *Steyermark 53610* (US, NY). NAPO: Lago Agrio–Baeza, 1,940–2,000 m, 0°15′S, 77°45′W, *Oellgaard et al. 35767* (AAU); Quito–Baeza, S of rd. above jct. of rds. to Baeza & Lago Agrio, 1,800 m, *Croat 58491* (K, MO, QCA, RSA, US, VEN); Lago Agrio–Baeza, 32.8 km E of Baeza turn-off, 1,840 m, 0°17′S, 77°46′W, *Croat 58730* (B, CM, MO, QCA); Baeza–jct. of road to Lago Agrio, 2,500 m, *Croat 49439* (MO, NY, QCA); Baeza–Tena, 37.7 km S of Baeza, 59 km N of Archidona, 1,700 m, 0°36′S, 77°51′W, *Croat 58781* (CAS, MO, QCA); Cantón Archidona, Carretera Hollín–Loreto, Km 50, Guagua Sumaco, 1,000 m, *Cerón & Hurtado 6565* (MO); Km 25, Challua Yacu, 1,200 m, *Cerón & Hurtado 6455* (MO); Baeza–Lago Agrio, 19.7 km NE of El Chaco, 39 km NE of jct. of road to Tena, 1,750 m, *Croat 58529* (MO, QCA); Río Oyacachi, 1,620 m, 0°20′S, 77°55′W, *Croat 50297* (M, MO); Km 142, 1,800 m, *Croat 49454* (IBE, MO, NY); Cerro Antisana, 1 mi. NE of Borja, NE of Baeza, 1,850 m, 0°25′S, 77°50′W, *Grubb et al. 1267c* (K); Cordillera de Guacamayos, S slope, Baeza–Tena, above Jondachi, 1,500 m, *Harling & Andersson 16342* (AAU, MO); Volcán Sumaco, Cotundo–Coca, 15 km E of Baeza–Tena road, 1,300 m, 0°40′S, 77°40′W, *Palacios & Neill 1559* (MO). TUNGURAHUA: Río Negro, 1,200 m, 1°24′S, 78°13′W, *Harling & Andersson 17240* (GB). ZAMORA–CHINCHIPE: La Saquea–Yacuambi, 1 km N of Chapintza road, 1,100 m, *Harling & Andersson 23868* (GB). PERU. AMAZONAS: Serranía de Bagua, 17 km E of La Peca, 1,850–1,900 m, *Gentry et al. 22969* (MO); Prov. Bagua, 20 km on trail E of La Peca, 2,190 m, *Barbour 2735*, *2746* (MO). CAJAMARCA: Cutervo, San Andrés de Cutervo, Parque Nacional de Cutervo, between Saucedal and Chorro Blanco, 2,250 m, *Díaz & Osores 2932* (MO, USM); between Saucedal and Pajonal, 2,300 m, *Díaz & Osores 2979* (MO, USM). SAN MARTÍN: Moyobamba–Chachapoyas, Km 380, E of Río Nieva, 1,750 m, 5°44′S, 77°32′W, *Croat 58215* (MO, USM); Rioja–Pomacocha, Km 291, Venceremos, 1,850 m, 5°45′S, 77°40′W, *Gentry et al. 45504* (MO).

Anthurium plowmanii Croat, Candollea 42(2): 811–813. 1987. TYPE: Brazil. Amazonas: Mpo. Manaus, Chacaras de Taruma, 16 km NW of Manaus, 60 m, 2°51′S, 59°50′W, *Croat & Nelson 53563* (holotype, INPA; isotypes, B, G, K, IBE, MO, NY, RSA, US). Figures 237–239, 240, 258.

Epiphytic or epilithic; stem 10–30 cm long, 2.5–6 cm diam.; leaf scars ca. 4 cm wide; roots dense, ascending or descending, whitish green, shortly pubescent, short or elongate, tapered, 4–6 mm diam.; cataphylls coriaceous, 5–20(27) cm long, obtuse to acute at apex, drying reddish brown (B & K yellow-red 4/5), persisting as a reticulum of fibers, the epidermis drying thin and flaking off, revealing the thin, reddish brown, hairlike fibers beneath. *Leaves* erect to spreading, reported to 2 m long; petioles (7.5)10–40(50) cm long, 4–20 mm diam., U- to C-shaped, narrowly and obtusely sulcate adaxially with the margins blunt, rounded to rarely 1–2-ribbed abaxially, the surface pale-speckled; geniculum thicker than petiole, becoming fissured transversely with age, 0.5–2 cm long; sheath ca. 3 cm long; blades coriaceous, obovate to oblanceolate or elliptic to broadly elliptic, acuminate to obtuse at apex (the acumen inrolled or downturned), acute to attenuate (rarely long-attenuate), or obtuse at base, (24)40–125(200) cm

long, (6)20–55(66) cm wide, broadest at or near the middle, the margins prominently and broadly undulate; upper surface matte to semiglossy or weakly glossy, dark green, lower surface matte to weakly glossy, concolorous with the upper surface or slightly paler; midrib flat to angular at base, becoming prominently and convexly raised (almost round-raised, with narrow sulcus along each side) and narrowly angular toward the apex above, prominently thicker than broad to weakly 2–3-ribbed at base, becoming prominently and convexly raised toward the apex below; primary lateral veins (4)7–15 per side, departing midrib at (30)45–65° angle, ascending ± straight to the margin or slightly arcuate-ascending, prominently and convexly raised above and below, more so below; interprimary veins obscure; collective vein arising from near the apex or absent, if present flat to weakly sunken above, flat to weakly raised below, 4–6 mm from margin. *Inflorescences* erect to erect-spreading; peduncle (2)6–32 cm long, 3–9 mm diam., 0.2–0.3× as long as petiole, plain green or heavily to slightly tinged with red, purple, or maroon, terete to ribbed abaxially; spathe semi-erect to spreading to reflexed or rolled up, subcoriaceous to coriaceous, violet purple or green tinged with purple, lanceolate to broadly lanceolate, (4)5–26(29) cm long, (0.5)1–3.5 cm wide, broadest near the base, inserted at 40–55° angle on peduncle, acute to long-acuminate at apex (the acumen inrolled), obtuse to acute or sometimes slightly decurrent at base, the margins meeting unequally, thick, rolling down at edges; stipe 1–20 mm long in front, 1–3 mm long in back; spadix green to dull maroon to green tinged with violet to violet-purple, tapered to cylindroid, longer than peduncle, (7)10–46 cm long, 10–20 mm diam. near base, 3–10 mm diam. near apex, broadest at the base; flowers square to rhombic, 1.5–2.5 mm long, 1.1–2.5 mm wide, the sides ± straight to jaggedly sigmoid; (8)10–16(18) flowers visible in principal spiral, 6–10 in alternate spiral; tepals matte, minutely and densely papillate; lateral tepals 0.6–1.2 mm wide, the inner margins straight to convex, the outer margins 2-sided; pistils emergent, weakly raised before the stamens emerge, reddish to dark purple; stigma linear, 0.2–0.6 mm long; stamens emerging in a regular sequence from the base, the laterals preceding the alternates by ca. 5 spirals; filaments holding anthers above the tepals; anthers orange, ca. 0.6–0.8 mm long, 0.8–0.9 mm wide, inclined over and obscuring the pistil; thecae ellipsoid to obovoid, not divaricate; pollen yellow to orange fading to cream, yeasty-scented. *Infructescence* erect to pendent; spathe deciduous, leaving a coarse scar; spadix 5–25 cm long, 1–3 cm diam., the apical ⅓ withered, fruits developing in the lower ⅔ only; berries red, oblong-obovoid, slightly rounded at apex (the stigma button-shaped), 8–12 mm long, 3–6 mm diam.; mesocarp juicy, sweet, translucent; seeds 1–2 per berry, brown, densely speckled with translucent dots in rehydrated specimens, oblong to ovoid, 5–6 mm long, 2–3 mm diam., 1.5–2 mm thick, with sticky appendage at the apex (forked in rehydrated specimens).

Anthurium plowmanii ranges from Brazil (Acre, Amazonas, Mato Grosso, and Rondônia) to Bolivia (La Paz, Pando, and Santa Cruz), Paraguay (Amambay) and Peru (San Martín) at 50–900 m, typically in the dry forest life zones of Peru and the varzea and terra firme habitats of Brazil.

A large epiphytic or epilithic species, *A. plowmanii* is unusual in sect. *Pachyneurium* by virtue of its spadix, which is longer than (or rarely as long as) the peduncle. This feature is shared only with *A. solomonii* (see discussion under the latter for distinctions from *A. plowmanii*). Also distinctive are the C- to U-shaped petioles with blunt adaxial margins, otherwise of rare occurrence in the section. Typical of *A. plowmanii* is the gradual disintegration of the distal (presumably unpollinated) portion of the spadix in the fruiting stage with, at most, only the weathered axis remaining. Fruiting spadices are thus regularly much shorter than flowering spadices, quite opposite the normal situation in the section.

Some atypical material of cultivated origin is included here under *A. plowmanii*, such as *Casari 165*, which differs in its unusually coriaceous leaf blades that are oblong-attenuate (vs. usually acute to attenuate) at the bases. The infructescence and other features are, however, typical. *Croat 53701*, received from and cultivated at the sitio of Roberto Burle-Marx in Rio de Janeiro, Brazil, has lanceolate (vs. obovate to elliptic) leaf blades with unusually prominent venation and notably olive-green coloration on drying. Photos of this collection taken in Brazil closely resemble typical material, however.

BOLIVIA. WITHOUT LOCALITY: collected by F. Fuchs of Homestead, Florida, *Croat 53542* (GH, MO, UCLA). COCHABAMBA: Río Grande, *Velasco 7192* (NY). LA PAZ: Prov. Iturralde, *Solomon 16940* (MO); Luisita, 180 m, 13°05′S, 67°15′W, *Haase 266* (MO). PANDO: Lago Bay, black water lake formed by Río Arroyo, upstream from junction with Río Manuripi, 11°57′S, 68°40′W, *Sperling & King, 6564* (MO); Río Madeira, Cachoeiras Misericordia–Madeira, *Prance et al. 6598* (NY); 4 km above Abuña, *Prance et al. 6271* (INPA); Río Madre de Dios, Federico Roman, Loma Alta, 110 m, *Solomon 17068* (MO); Manuripi, upstream from Riberalta, 220 m, 10°55′S,

66°8′W, *Daly et al. 2042* (NY). SANTA CRUZ: *Weddell 3518* (P); Andres Ibanez, 12 km E of Santa Cruz--Cotoca, 375 m, 17°46–47′S, 63°04′W, *Nee 34009* (NY); ca. 40 km S of Asunción dos Guarayos, Nufles de Chaves, 15°55′S, 63°05′W, *Hopkins et al. 218* (MO); Serranía de Santiago, N slope, Chiquitos, 10 km ENE of Santiago de Chiquitos, 900 m, 18°20′S, 59°28′W, *Daly et al. 2243* (MO). BRAZIL. ACRE: Mpo. Sena Madureira. Rio Iaco, *Cid & Nelson 2757* (INPA). AMAZONAS: cultivated, INPA campus, Manaus, *Nelson 1335* (MO); N of Coreiro, 10 km downstream from Manaus, *Leppard 1645* (K); Solimões, Mamia, *Kuhlman 1191* (RB); Lago do Janauari, Manaus, *Coelho 638* (INPA); Manaus, 50 m, *Croat 53563* (B, G, IBE, INPA, K, MO, NY, RSA, TEX, US); Rio Acre, behind Santa María, W bank of Rio Acre, Boca do Acre, *Prance et al. 2361* (INPA), *2371* (INPA, NY, US); Rio Madeira basin; Humayta, near Livramento, on Rio Livramento, *Krukoff 6767* (NY). MATO GROSSO: Aripuanã, Cidade Humboldt, 10°12′S, 59°21′W, *Rodrigues 9816* (INPA); Chapada dos Guimaraes, *Hutchison 8553* (UEC); Porto Espiridião–Porto Velho, 286 km NW of Porto Esperidião, on BR-364-MT, *Hutchison 8602* (MO, UEC); Urucum, Corumba, 19°00′S, 57°35′W, *Pereira, Egler & Graziela 447* (RB); Serra Ricardo Franco, 350 m, 15°S, 60°W, *Windisch 1514* (K). RIO DE JANEIRO: cultivated, Rio de Janeiro, base of Pedra Bonita, Rue Elviro Niemeyer 14, *Casari 165* (GUA); cultivated by Burle Marx, San Carlos, *Croat 53701, 53710* (MO). RONDÔNIA: Rio Madeira, Riberão, Cachoeira Misericordia, *Prance et al. 6721* (INPA, NY, US); Abunã–Penha Colorado, *Prance et al. 8725* (INPA, NY, US); Mpo. Costa Marques, ca. 5 km NW of Costa Marques, 150 m, 12°25′S, 64°14′W, *Nee 34548* (NY). PARAGUAY. AMAMBAY: Cerro Chanchito, 22°26′S, 56°3′W, *Schinini & Bordas 20398* (K); Cerro Memby, cultivated in Asunción, *Krapovickas & Schinini 28533* (K); Sierra de Amambay, Montes Barrancas, Piedra Esperanza, *Hassler 10640* (G); Parque Nacional Cerro Cora, 300 m, 22°39′S, 56°03′W, *Solomon et al. 6987* (MO); summit of Cerro Muralla, *Casas 3955* (NY). PERU. WITHOUT LOCALITY: cultivated at SEL, #81-76-10, and at MO, *Plowman 6011 B* (MO, NY, TEX). SAN MARTÍN: Tarapoto–Juanjui, Km 24–25, 300–500 m, 6°40′S, 76°20′W, *Croat 50987* (F, MO), *Plowman 6044* (GH); Río Huallaga, 29–31 km S of Tarapoto, near El Abra, 450–540 m, 6°40′S, 76°20′W, *Gentry & Smith 45091* (MO); 350 m, 6°35′S, 76°25′W, *Gentry et al. 37733* (MO); Río Mayo, 6 km S of Tarapoto–Moyobamba Rd. at Km 15, Cunumbigue village, 350 m, 6°23′S, 76°39′W, *Croat 51094* (CM, F, K, MO, RSA).

Anthurium pranceanum Croat, sp. nov. TYPE: Brazil. Acre: Rio Moa between Cachoeira Grande and Serra de Moa village, *Prance et al. 12640* (holotype, INPA; isotypes, F, K, NY, U, US). Figure 241.

Planta terrestris; internodia brevia, 1–1.5 cm diam.; cataphyllum lanceolatum, persistens semi-intactum; petiolus 35–65 cm longus, 4–8 mm diam., subteres, adaxile sulcatus; lamina ovato-elliptica ad ovata, 40–70 cm longa, 17–26 cm lata; geniculum 4–20 cm remotum; pedunculus 24–40 cm longus; spatha lanceolata, violaceus, ca. 4 cm longa, 1.2 cm lata; stipes 1–10 cm longus; spadix violaceus, ca. 5 cm longus, 5–6 mm diam.

Description based on dried material only. Terrestrial; stem 1–1.5 cm diam.; roots densely and finely pubescent, ca. 2–4 mm diam.; cataphylls subcoriaceous, lanceolate, ca. 10 cm long, acute at apex, reddish brown, persisting semi-intact. *Leaves* with petioles 35–65 cm long, 4–8 mm diam., subterete, sulcate adaxially, rounded abaxially; geniculum slightly darker than petiole, ca. 1 cm long, appearing remote from base of blade by 4–20 cm; blades moderately coriaceous, ovate-elliptic to ovate, shortly acuminate at apex, broadly rounded then abruptly attenuate at base, 40–70 cm long, 17–26 cm wide, broadest at or below the middle, lower surface dark glandular-punctate; both surfaces green to yellowish green; midrib convexly raised above, acutely raised below; primary lateral veins 6–9 per side, departing midrib at 50–60° angle, ± straight, becoming arcuate near the margin, apparently convexly raised above and below; tertiary veins weakly raised; collective vein arising from about the middle of the blade, apparently sunken above, raised below, less prominent than primary lateral veins, 7–24 mm from margin. *Inflorescences* erect, shorter than leaves; peduncle 24–40 cm long; ca. 2–5 mm diam., about half as long as petiole, terete; spathe recurled, membranous, violet, lanceolate, ca. 4 cm long, ca. 1.2 cm wide, broadest near the base, narrowly acute at base; stipe 15–28 mm long in front, 1–10 mm long in back; spadix violet, weakly tapered, ca. 7.7 cm long, 5–6 mm diam. near base, ca. 3 mm diam. near apex; flowers rhombic, ca. 2 mm in both directions, the sides ± straight to smoothly sigmoid; 4–6 flowers visible in either spiral; tepals smooth when dried; lateral tepals 1 mm wide, the inner margins straight, the outer margins 2-sided. *Infructescence* not seen.

Anthurium pranceanum is known only from the type collection made near the Rio Moa in Acre, Brazil, below 300 m.

This species is distinguished by its ovate to ovate-elliptic leaf blades which are dark glandular-punctate below and have the geniculum situated 4–20 cm below the base of the blade.

Anthurium pranceanum is apparently most closely related to *A. krukovii*, which also has a remote geniculum but lacks dark glandular punctations on the lower surface of the leaf blade. It also bears some resemblance to *A. bonplandii* subsp. *bonplandii*, which occurs further north in the Amazon basin and often has similar dark glandular punctations. The latter differs in its proportionately narrower leaf blades which are acute to

attenuate at the base and do not have a remote geniculum.

The species is named in honor of G. T. Prance, one of the foremost explorers of Brazilian Amazonia, who has collected numerous Brazilian Araceae, including the type of *Anthurium pranceanum*.

BRAZIL. ACRE: Rio Moa, Cachoeira Grande–Serra da Moa village, *Prance et al. 12640* (F, INPA, NY, U, US).

Anthurium prolatum Croat & R. A. Baker, Brenesia 16(Suppl. 1): 72. 1979. TYPE: Costa Rica. Heredia: Istarú Farm, Tirimbina, Sarapiquí, 220 m, *Lent 2140* (holotype, F-1724125). Figures 242–245, 259.

Epiphytic; stem short, 1–2.5 cm diam.; roots few, descending, pale greenish, ± smooth, slender, 3–5 mm diam.; cataphylls moderately coriaceous, narrowly lanceolate, 7.5–36 cm long, acute at apex with subapical apiculum, medium green, drying tan, persisting as fine linear fibers. *Leaves* spreading to pendent; petioles 1–35 cm long, 3–6 mm diam., terete to subterete, weakly flattened to flattened or rounded adaxially, rounded abaxially, the surface weakly pale-speckled; geniculum thicker and paler than petiole, 0.5–1 cm long; blades subcoriaceous to moderately coriaceous, strap-shaped to narrowly oblong-elliptic, long-acuminate at apex (the acumen weakly apiculate), narrowly acute to obtuse to narrowly rounded at base, (35)83–142 cm long, 3.5–10 cm wide, broadest at or near the middle, the margins weakly undulate; upper surface semiglossy, dark green, lower surface semiglossy to glossy, paler; midrib above acutely raised at base, becoming weakly sunken toward the apex, below prominently higher than broad at base, becoming convexly raised toward the apex and paler than surface; primary lateral veins more than 15 per side, departing midrib at ca. 55° angle, ± straight, obscure to weakly sunken above, somewhat raised and darker than surface below; interprimary veins numerous, almost as conspicuous as primary lateral veins; tertiary veins obscure above, somewhat darker than surface below; reticulate veins prominulous above and below; collective vein arising from near the base, sunken above, weakly raised and darker than surface below, more prominent than primary lateral veins, 3–4 mm from margin. *Inflorescences* with peduncle to 39 cm long, ca. 9 mm diam., slightly longer than petiole, several-ribbed on drying; spathe spreading, subcoriaceous, pale green, linear-lanceolate, to 29 cm long, ca. 1.5 cm wide, broadest near the base, inserted at 70° angle on peduncle, acuminate at apex (the acumen minutely inrolled), acute at base; spadix brown (fide labels) probably greenish purple, sessile, very narrowly cylindroid, slightly tapered at apex, to 60 cm long, 7–8 mm diam. near base, ca. 4 mm diam. near apex; flowers (dry) rhombic, (2.7)3.4–4.5 mm long, 1.8–2.2 mm wide, the sides jaggedly sigmoid; 7–8 flowers visible in principal spiral, 5–6 in alternate spiral; tepals epunctate, smooth; lateral tepals 2.2–5 mm wide, the inner margins convex; pistils rectangular, green; stigma oblong, ca. 0.7 mm long; filaments retracting on drying. *Infructescence* to more than 30 cm long, probably with orange berries.

Anthurium prolatum is known from western Panama and Costa Rica (in Alajuela, Limón, Heredia, and Cartago provinces) in tropical wet forest at 350–1,000 m.

This species can be distinguished by the unusual, very long and narrow leaves, cataphylls, spadix, and spathe. It is most easily confused with *A. protensum*, differing in its spadix, which is more than twice as long as any observed for *A. protensum*; its spathe, which is considerably narrower and lacking the purple markings characteristic of *A. protensum*; and its flowers, which are twice as long as those of *A. protensum*. In addition, the much more common *A. protensum* is most frequent at about 1,800 m.

COSTA RICA. ALAJUELA: Naranjo–Aguas Zarcas, 8.5 km NE of Villa Quesada, Hwy. 15, 600 m, *Croat 46979* (MO). CARTAGO: 1.5 mi. E of Cachí, 10.2 mi. NE of junction at Paraiso, *Croat 47087* (MO). HEREDIA: Tirimbina, Sarapiquí, Istarú Farm, *Lent 2140* (F). LIMÓN: Lago Dabagri, W coast, toward Río Llei, 1,000 m, 9°38′N, 83°18′W, *Gómez et al. 23155* (B, K, MO); Río Tor Amarillo, 6 km SW of Guapiles, 400 m, *Jimenez 2113* (F). SAN JOSÉ: Parque Nacional Braulio Carrillo, entrance–Río Sucio, Estación Carrillo, 400–1,500 m, 10°5–10′N, 84°57–60′W, *Hammel & Trainer 14266* (MO). PANAMA. BOCAS DEL TORO: Fortuna–Chiriquí Grande, 550–600 m, ca. 8°48′N, 82°10′W, *McPherson 9154* (MO).

Anthurium protensum Schott, Oesterr. Bot. Z. 8: 181. 1858.

a. Anthurium protensum subsp. **protensum**. TYPE: Costa Rica. Heredia: Volcán Barba, 2,500–2,700 m, *Oersted 1992* (destroyed?; illustrated by Schott Aroideae 427). Figures 246–248, 260, 261.

Anthurium costaricense Engl., Bot. Jahrb. Syst. 25: 398. 1898. TYPE: Costa Rica. Cartago: above Agua Cali-

ente, 1,800 m, *Lehmann s.n.* (holotype, B; isotype, P).

Anthurium joseanum Engl., Pflanzenr. IV 23B(Heft 21): 68. 1905. TYPE: Costa Rica. Cartago: Las Vueltas, Tucurrique, 635 m, *Tonduz 12818* (holotype, B; isotypes, P, US).

Epiphytic; stem often pendent, less than 20 cm long, 1–2 cm diam.; roots descending, brownish to green, smooth, thick and moderately elongate, 5–7 mm diam.; cataphylls subcoriaceous, narrowly lanceolate, (8)11–30 cm long, obtuse to acuminate and long-apiculate at apex, pale green, drying pale tan, persisting intact, soon dilacerating into a reticulum of fine fibers. *Leaves* spreading to pendent; petioles (6)10–35 cm long, 3–7 mm diam., subterete to bluntly angular, sometimes flattened or weakly sulcate adaxially, the surface sparsely pale-speckled; geniculum paler and slightly thicker than petiole, becoming fissured transversely with age, 1–2 cm long; blades subcoriaceous, strap-shaped to oblong-elliptic, long-acuminate at apex (the acumen weakly apiculate), acute to obtuse to narrowly rounded at base, (18)32–80 cm long, (2.5)4–11.5 cm wide, the margins undulate; upper surface matte to semiglossy, dark to medium green, lower surface semiglossy, paler to almost concolorous with the upper surface, drying greenish and matte; midrib convexly raised at base, becoming narrowly raised and then weakly sunken toward the apex above, higher than broad at base, becoming convexly raised toward the apex below, paler than surface above and below; primary lateral veins more than 15 per side, departing midrib at 40–70° angle, sunken to obscure above, flat to raised and darker than surface below; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins weakly visible above and below; collective vein arising from near the base, sunken above, raised and somewhat darker than surface below, equally as prominent as primary lateral veins, 2–5 mm from margin. *Inflorescences* spreading-pendent, shorter than leaves; peduncle (13)15–49 cm long, 6–7 mm diam., 0.6–1.8× as long as petiole, pale-speckled, terete; spathe erect to reflexed, subcoriaceous, yellow-green to purple to maroon, oblong-lanceolate to lanceolate, (4.5)10–19 cm long, 1.7–4 cm wide, acuminate to long-acuminate at apex (the acumen inrolled), rounded to obtuse at base; spadix greenish to pale violet-purple to purplish gray, usually glaucous, long-tapered, prominently curved, (4)7–19 cm long, 5–9 mm diam. near base, 2–4 mm diam. near apex; flowers rhombic to 4-lobed, 2.2–2.7 mm long, 1.8–2.2 mm wide, drying 1.5–1.8 mm diam.; 4–9 flowers visible in principal spiral, 6–12 in alternate spiral; tepals densely and minutely papillate, weakly pale-punctate; pistils emergent, densely and minutely papillate, green; stigma linear, droplets appearing 2–4 days before stamens emerge; stamens emerging from the base, the laterals preceding the alternates by 30–34 spirals, the 3rd stamen preceding the 4th by 5–6 spirals, held in a tight cluster above the pistil; anthers yellow to tan, 0.5–0.6 mm long, 0.6–0.7 mm wide; thecae ellipsoid, slightly divaricate; pollen pale orange fading to white. *Infructescence* with spadix 14–32 cm long; berries orange, ovoid to oblong-ovoid, acute to beaked at apex, (6.4)8–13 mm long, (3.9)4.5–8 mm diam.; seeds 2 per berry, yellow to pale brown, oblong to semi-ovoid, flattened, (3.4)3.7–6 mm long, (1.8)2.5–4.5 mm diam., (1.2)1.6–3 mm thick, with a gelatinous, amber appendage.

This species is found in Costa Rica and Panama from 635 to 2,700 m, principally in premontane rain and lower montane rain forest life zones.

Anthurium protensum is distinguished by its cataphylls weathering to a reticulum of fibers, its elongate, narrow leaf blades with many primary lateral veins, its more or less terete petiole, the long, ovate to lanceolate spathe, pale violet-purple to lavender or greenish spadix and orange berries.

This species is closely related to *A. prolatum*, *A. brenesii*, and *A. seibertii*, all with similar, elongate leaves. See the commentary following those species for distinguishing characteristics.

Anthurium protensum comprises two subspecies. The typical subspecies occurs mostly in Costa Rica (also in western Panama), while subsp. *arcuatum* occurs only in Panama, ranging from Chiriquí to Veraguas at 1,300 to 1,750 m in premontane rainforest. The latter differs in being an erect plant with smaller leaves with fewer, more prominent, sunken veins and an acute lower midrib, an arching inflorescence with shorter, usually ovate spathe and a smaller spadix.

A third subspecies may be represented as well. Some collections have slender green spadices sometimes two or more times longer than the spathe, a generally green spathe and glabrous tepals. Examples of this entity include *Croat 60444*, *McPherson 8026* and *8685* from Bocas del Toro Province in Panama, and *Croat 36714* and *Chacon 7*, from Cartago Province in Costa Rica. More typical collections have the spadix more short-tapered, frequently tinged purple, about as long as the spathe or even shorter than the spathe, and tepals covered with a thin, waxy layer. The spathe in this latter group is usually heavily tinged purple. Examples of these plants include *Croat 44501*,

47113, *Grayum 3867*, and *Lehmann 1756* (the type of *A. costaricensis*). Because the types of both *A. protensum* and *A. costaricensis* (considered a synonym of the former) correspond to the more commonly collected variant, the plants with the longer spadices and glabrous tepals, if they prove to be distinct, would perhaps represent a new subspecies.

COSTA RICA. WITHOUT LOCALITY: *Lehmann 1756* (B). ALAJUELA: Zapote, *Smith 1268* (NY); 11 mi. NW of Zarcero, Finca Los Ensayos, 900 m, *Croat 43533* (CM, MO); Zarcero, *Smith A692* (MO); Cordillera de Tilarán, Finca Peñas Blancas, E slope Cerros Centinelas, Monte Verde Reserve, 1,300–1,450 m, 10°18′N, 84°47′W, *Grayum 5364* (MO). ALAJUELA & PUNTARENAS: Monteverde, *Burger et al. 10792* (F); N side of Quebrada Cuecha near Sendero El Río, 1,560 m, 10°18′30″N, 84°47′50″W, *Hayworth 240* (WIS), 1,580 m, *Hayworth 222* (WIS). CARTAGO: Las Vueltas, Tucurrique, 635 m, *Tonduz 12818* (B, P, US); Moravia de Chirripó, Shiripi, 900–1,000 m, *Chacon 7* (MO); SE of Platanillo, Camino Raiz de Hule, 1,200–1,400 m, *Croat 36714* (F, DUKE, ENCB, GH, K, MEXU, MBM, MO, NY, PMA, RSA, SEL, TEX, US); Carpintera, *Brade 2513* (BR); La Cangreja, *Williams et al. 24182* (NY); NE of Pacayas, *Luteyn 3250* (DUKE); 6 km past town of Río Macho on road to Humo, Continental Divide, 1,600 m, 9°17′N, 83°45′W, *Hoover 1347* (MO); Río Grande de Orosi, suspension bridge-point opposite mouth of Quebrada Casa Blanca, Tapantí, 1,250 m, 9°46.5′N, 83°48′W, *Grayum & Jacobs 3776* (MO). GUANACASTE: La Palma, *Greenman & Greenman 5465* (MO). HEREDIA: N of Vara Blanca, *Maxon & Harvey 8304* (US), *Skutch 3706* (MICH, US); 4 mi. N of Vara Blanca, 1,350 m, *Croat 35566* (MO); San Rafael–Río San Rafael, 3 km E of Vara Blanca, 1,800 m, *Utley & Utley 4190* (MO); 1,720 m, *Rojas 513* (MO); N of Concepción, *Primack et al. 276* (DUKE); Braulio Carrillo Park, Zurquí, 1,800 m, *Gómez 20092* (MO); between Río Peje and Río Sardinal, 1,200–1,400 m, 10°15′N, 84°05′W, *Grayum & Herrera 7854* (MO); Cordillera Central, N slopes, Poas–Volcán Barba, Vara Blanca de Sarapiquí, 1,650 m, *Skutch 3652* (MICH, MO, NY); Río Pará Blanco, 1,600 m, 10°3′N, 84°1′W, *Lent 2874* (MO); Río Socorro, Sarapiquí–Cariblanco, 600–800 m, *Chacón & Herrera 1172* (MO). HEREDIA & SAN JOSÉ: Río Pará Blanco drainage, Cerro de Zurquí, 1,600–1,800 m, 10°3′N, 84°1′W, *Burger et al. 10290* (F, MO). LIMÓN: Cordillera de Talamanca, Río Tararia–NE Kámuk Páramo, Atlantic slope of Kámuk massif, 1,900–2,300 m, 9°14′N, 82°59′W, *Davidse & Herrera 29212* (MO). PUNTARENAS: SE of Santa Elena, *Almeda et al. 2031* (DUKE); headwaters of Río Bella Vista–Sitio Cotón (Cotoncito) on Río Cotón, 1,800–2,200 m, 9°49–57′N, 82°46–49′W, *Davidse et al. 25543* (MO); Monteverde, *Kennedy 605* (US), *Luteyn 3406* (DUKE); 1,500–1,550 m, *Haber 1164, 3897* (MO); Río San Luis valley, 900–1,000 m, *Haber et al. 8518* (CR); Cordillera de Tilarán, 1,550–1,720 m, *Almeda et al. 4972* (CAS, MO); Sendero El Río, Monteverde, 1,600 m, 10°18′N, 84°48′W, *Grayum & Sleeper 3867* (MO); valley of Río San Luis, just S of Monteverde, 1,000–1,200 m, 10°16′N, 84° 48′W, *Hammel & Haber 13906* (MO); Mike Fogden property, *Croat 46770* (B, MO), *Palmer 158* (NY); Santa Elena–Monteverde, 3.5 mi. from Santa Elena–Monteverde junction, near E edge of Monteverde Reserve, 1,350 m, *Croat 47113* (CM, MO); Río Barú, upper part, 201 m, *Gómez et al. 21523* (MO). SAN JOSÉ: Aserrí–Tarbaca, *Standley 41402* (US); Bajo La Hondura, *Lent 1446* (WIS), *Standley 36334* (US); 3 km N of Cascajal, 1,680 m, *Almeda & Anderson 5284* (CAS, MO); La Palma, *Luteyn 3301* (DUKE); Piedra, *Luteyn 3291* (DUKE); Parque Nacional Braulio Carrillo, Bajo La Hondura, 1,100–1,200 m, 10°4′N, 83°58′W, *Davidse et al. 23190* (MO); Río Claro–Paracito, Bajo La Hondura, 1,100–1,400 m, *Croat 44501* (MO); Santa María de Dota, 1,850 m, *Stork 1737* (MICH). PANAMA. BOCAS DEL TORO: Fortuna–Chiriquí Grande, 1.2 mi. N of Continental Divide, 5.3 mi. N of bridge over Fortuna Dam, 910 m, 8°44′N, 82°17′W, *Croat & Grayum 60444* (MO, PMA). CHIRIQUÍ: above Boquete, rd. to Bajo Mono and Alto Quiel, 1,650 m, 8°51′N, 82°29′W, *McPherson & Merello 8360* (K, MO).

b. Anthurium protensum subsp. **arcuatum** Croat, Ann. Missouri Bot. Gard. 14: 164, figs. 139 & 140. 1986. TYPE: Panama. Chiriquí: above San Félix along mining road, 25 mi. off Pan-American Highway, 1,500 m, *Croat 33138* (holotype, MO 231113; isotypes, F, K, PMA, US). Figures 249–251.

Usually epiphytic; stem less than 10 cm long, 0.7–1.8 cm diam., leaf scars 0.6 cm high, 1 cm wide; roots descending, greenish, pubescent, elongate, 3–4 mm diam.; cataphylls coriaceous, narrowly lanceolate, 3.4–7 cm long, green weakly tinged with red at margins, acute at apex, drying tan (B & K yellow 5/5), persisting intact, soon dilacerating into reticulum of fine fibers. *Leaves* spreading to pendent; petioles 10–32 cm long, 2–4 mm diam., subterete to bluntly D-shaped to quadrangular, sharply 4–5-ribbed and winged, flattened to weakly or prominently and narrowly sulcate adaxially, the margins sharply raised to winged, rounded to bluntly angular to sharply ribbed abaxially, the surface sparsely pale-speckled; geniculum slightly paler and thicker than petiole, 1–1.5 cm long; blades coriaceous to subcoriaceous, oblong to narrowly oblanceolate to narrowly elliptic or lanceolate, gradually long-acuminate at apex, obtuse to rounded at base, 19–51 cm long, 2.5–7.5 cm wide, broadest at or below middle; upper surface weakly glossy to semiglossy, dark green, lower surface semiglossy to glossy below, paler; midrib above convexly raised at base, becoming narrowly raised and eventually weakly sunken toward the apex, below acutely higher than broad at base, becoming sharply acute toward the apex, paler than surface above and below; primary lateral veins 7–12 per side, departing midrib at 45–50° angle, weakly arcuate to the collective vein, prominently to slightly sunken above, sharply to weakly raised and darker than surface below; interprimary veins

scarcely visible, sunken above, raised below; tertiary veins obscure above, sometimes weakly visible below; collective vein arising from the base, sunken above, moderately sharply raised below, equally as prominent as primary lateral veins, 2–5 mm from margin. *Inflorescences* erect to spreading, shorter than leaves; peduncle 13–38 cm long, 2–4 mm diam., usually longer than petioles, 0.5–2× as long as petioles, pale green sometimes tinged with reddish violet, terete to sharply 1-ribbed abaxially; spathe erect, curved over and hooding spadix, plain green or heavily tinged with reddish violet to reddish purple, ovate to broadly lanceolate, 4.5–14 cm long, 1.7–3.5 cm wide, broadest near the base, inserted at 70° angle on peduncle, long-acuminate to caudate at apex, obtuse to rounded or subcordate at base; stipe 5–15 mm long; spadix white to lavender (B & K purple 7/7.5) (also reported as light green becoming tan), cylindroid to weakly tapered, weakly curved, 2–9 cm long, 4–6 mm diam. near base, 3–4 mm diam. near apex; flowers rhombic to 4-lobed, (1.3)1.5–3 mm long, (1.3)1.6–2.8 mm wide, drying 1.7–1.9(2.2) mm wide; the sides jaggedly to smoothly sigmoid; 4–5 flowers visible in principal spiral, 5–8 in alternate spiral; tepals matte, minutely and densely papillate; lateral tepals 0.7–1.7 mm wide, the inner margins convex, the outer margins 2–3-sided; pistils scarcely emergent, papillate, pale green to pale violet-purple; stigma ellipsoid, 0.3–0.5 mm long, brushlike, droplets appearing briefly before stamens emerge; stamens emerging from the base, lateral stamens followed by alternates in a rapid succession, the laterals preceding the alternates by 1–2 spirals, held over and obscuring the pistil; anthers pale yellow, 0.4–0.5 mm long, 0.9–1 mm wide; thecae ellipsoid, brown, slightly divaricate; pollen pale yellow fading to creamy white. *Infructescence* pendent; spadix to 7 cm long, 2.5 cm diam.; berries bright orange, ovoid, beaked at apex, 6–9 mm long, 5–6 mm diam.; mesocarp pulpy, orange; seeds 2 per berry, creamy white, ovoid-ellipsoid, 3–3.2 mm long, 2.2–2.3 mm diam., 1.5 mm thick, enclosed in transparent, sticky envelope ca. 5 mm long, extending further beyond the apex than the base.

Anthurium protensum subsp. *arcuatum* is known principally from western Panama in premontane rainforest at 1,100–2,000 m. A single collection from Monteverde is apparently also included in this taxon even though it has not been collected elsewhere in Costa Rica.

This taxon is distinguished by its slender, short stem, more or less oblong leaf blades that are usually spreading and weakly arched, and by its usually arched inflorescence. Also characteristic is the usually lavender, greenish white or purplish violet spadix, and its ovate to broadly lanceolate, frequently purplish spathe that usually curves over and hoods the spadix.

The few cultivated collections of *Anthurium protensum* subsp. *protensum* and subsp. *arcuatum* are markedly different, but herbarium material is more difficult to separate. Subspecies *protensum* differs from subsp. *arcuatum* in having typically much larger leaf blades, rarely less than 50 cm long, with the primary lateral veins more numerous and less conspicuously sunken on the upper surface (scarcely more prominently sunken than the interprimary veins). In addition, the lower midrib is convex and the plant typically has a lanceolate spathe, a much longer, narrowly tapered spadix (usually more than 9 cm long), and an infructescence usually 20–30 cm long. Subspecies *protensum* is also usually a pendent or nearly pendent plant, whereas subsp. *arcuatum* is usually erect.

Subspecies *arcuatum* rarely has leaf blades more than 50 cm long, relatively fewer, sharply sunken primary lateral veins, an acutely raised lower midrib, a typically ovate spathe, with a spadix usually less than 5 cm long, and the infructescence less than 7 cm long.

COSTA RICA. PUNTARENAS: Monteverde Cloud Forest Reserve, along road to Peñas Blancas Valley, ca. ¼ mi. E of station, ca. 1,520 m, *Lesica & Antibus 4184* (CR, MO). PANAMA. BOCAS DEL TORO: Cerro Pate Macho, ENE of mountain, *Hammel 6254* (MO); Fortuna Road, road branching N off main Fortuna–Chiriquí Grande Hwy., 1.1 mi. from main road, 1,200 m, 8°44′N, 82°17′W, *Croat & Grayum 60295* (MO); Río Culebra, 5 km ENE of Cerro Pate Macho, 1,660 m, *Hammel 6136* (MO). CHIRIQUÍ: Boquete Region, Boquete, *Pittier 3062* (US); 9 km past divide in road to Alto Quiel from Boquete, 1,930 m, 8°49′N, 82°28′W, *Hoover 1341* (MO); Cerro Colorado, along mining road 18–27 mi. off Pan-Am Hwy., above Chamí or turnoff to Escopeta, above San Félix, 1,200–1,500 m, *Croat 33138* (F, K, MO, PMA, US); border of Chiriquí and Bocas del Toro provinces, 1,500–1,750 m, *Folsom et al. 4693* (MO); 1,170–1,250 m, 8°45′N, 82°18′W, *Croat 66839* (MO); along mining road 20 mi. above bridge over Río San Félix, near village of San Félix, 2,000 m, *Croat 48461* (MO); on upper mining road 20–28 mi. from San Félix, 1,200–1,500 m, *Croat 33369* (MO); 50 km N of San Félix on Continental Divide, 1,200–1,500 m, *Mori & Dressler 7770* (MO); along road above San Félix, 30 km above bridge over Río San Félix, 1,610–1,670 m, *Croat 37111, 37132* (MO); Cerro Horqueta, *Dwyer 8749* (DUKE), *Pittier 3160* (NY), *3161* (US); Cerro Punta, *Wilbur et al. 13081, 15235, 15236, 15252, 15377* (DUKE); Fortuna Road, Fortuna Lake–Chiriquí Grande, 4.5–5 km N of dam over Fortuna Lake, 1,100–1,135 m, *Croat & Grayum 60077* (B, CM, K, MO, PMA); trail along Continental Divide to W of Oleoducto road, Fortuna Dam, 1,200–1,500 m, 8°47′N, 82°13′W, *Churchill 5306* (MO); Río Chiriquí

Viejo, upper part, Monte Lirio, *Seibert 172* (K, NY). VERAGUAS: Santa Fe Region, Cerro Arizona, 1,330 m, *Hammel & Kress 8570* (MO); Cerro Tute, above Escuela Agrícola Alto Piedra, 800–1,450 m, *Croat 48964* (F, MO, PMA, US), *Folsom & Mauseth 8344* (MO), *Knapp & Dressler 5407* (MO), *Knapp & Kress 4353* (MO), *Sytsma & Andersson 4587* (MO).

Anthurium pseudospectabile Croat, Monogr. Syst. Bot. Missouri Bot. Gard. 14: 165. 1986. TYPE: Panama. Chiriquí: along road between Gaulaca and Fortuna Dam site, 8.3 mi. NW of Los Planes de Hornito, 8°44′N, 82°16′W, 1,260 m, *Croat 49942* (holotype, MO 2769003-005; isotypes, B, K, NY, PMA, SEL, W). Figures 252–254.

Usually epiphytic; stem ± slender, less than 30 cm long, 1.5–5 cm diam.; leaf scars 2–4 cm wide; roots few, spreading to descending, pale grayish to pale tan, occasionally greenish, somewhat pubescent, thick and elongate, tapered, 3–6 mm diam.; cataphylls coriaceous to subcoriaceous, lanceolate, stiffly erect, 19–37 cm long, acute to obtuse or ± rounded at apex, with subapical apiculum to ca. 4 mm long, light green, drying orange brown to tan, persisting intact, eventually as a reticulum of fibers. *Leaves* spreading to pendent; petioles 14–60 cm long, 7–12 mm diam., subterete to bluntly 4-sided, flattened to weakly and broadly sulcate adaxially, rounded abaxially, the surface pale-speckled; geniculum thicker and slightly paler than petiole, 1–3 cm long; blades subcoriaceous to coriaceous, oblong to oblong-elliptic, gradually acuminate at apex (the acumen weakly apiculate), decurrent to obtuse to truncate or subcordate at base, 45–150 cm long, 12–45 cm wide, broadest at or just below the middle, the margins weakly undulate; upper surface matte to semiglossy, dark green, lower surface semiglossy to glossy, slightly paler; midrib obtusely angular, becoming flat toward the apex above, prominently convex to round-raised, conspicuously paler than surface below; primary lateral veins up to 40 per side, departing midrib at 35–75° angle, straight to weakly arcuate to the collective vein, raised above in grooves, prominently raised below; interprimary veins almost as conspicuous as primary lateral veins, flat to weakly sunken above, raised below; tertiary veins obscure above, slightly darker than surface and weakly raised below; collective vein arising from near the base, sunken above, prominently raised below, equally as prominent as primary lateral veins, 2–5 mm from margin. *Inflorescences* spreading-pendent; peduncle 13–36 cm long, 5–9 mm diam., equaling up to 1.5× as long as petiole, terete to weakly quadrangular with blunt margins; spathe usually twisted or recurled, moderately coriaceous, green below, heavily tinged with purple above, lanceolate, 10–32 cm long, 2.5–7 cm wide, broadest near base, inserted at 45–60° angle on peduncle, gradually acuminate at apex, rounded to cordate at base; spadix yellowish green to green, sessile, narrowly tapered, 15–38 cm long, 8–12 mm diam. near base, 3–5 mm diam. near apex; flowers rhombic, ca. 3.5 mm long, 2.7–3 mm wide, the sides straight to weakly sigmoid; 4–7 flowers visible in principal spiral, 6–9 in alternate spiral; tepals matte, minutely papillate; lateral tepals 1.8–2 mm wide, the inner margins convex, turned up against the pistil; pistils early emergent, pale green; stigma linear, 0.6 mm long; stamens emerging ± rapidly from the base, arranged in a loose cluster around pistil; filaments ca. 0.3 mm long, ca. 0.5 mm wide; anthers white; thecae oblong, scarcely divaricate; pollen white. *Infructescence* pendent; berries orange, oblong-ellipsoid, 10–12 mm long, 5–6 mm diam.

Anthurium pseudospectabile is endemic to Panama at (590)1,000 to 1,600 m in a region that is probably premontane wet or premontane rain forest.

This species is distinguished by its pendent habit and its large, almost strap-shaped, many-veined blades with undulate margins. Also characteristic are the short-pedunculate inflorescence with a spreading, usually twisted and contorted green to purple spathe, the weakly protruding tepals, exserted stamens, early-emergent pistils, and orange berries.

Anthurium pseudospectabile is closely related to *A. spectabile*, from Costa Rica, but the latter has proportionately broader leaf blades which generally lack the undulate margins, and a petiole that is markedly quadrangular in cross section.

PANAMA. BOCAS DEL TORO: Cerro Colorado, trail along quebrada 7.5 mi. from Chamí, 1,220–1,250 m, 8°35′N, 81°45′W, *McPherson 8853* (MO); Fortuna Dam area, *Correa et al. 2664* (PMA); Oleoducto Road, Continental Divide, 1,000 m, *Churchill et al. 4647* (MO), *4648* (MO, PMA); vic. Fortuna Dam, Continental Divide, trail west of highway, 1,250 m, *McPherson 11626* (MO); Fortuna–Chiriquí Grande, 8.5 mi. N of bridge over Fortuna Lake, 4.3 km N of Continental Divide, 590 m, *Croat & Grayum 60203* (CM, MO); road branching N off main Fortuna–Chiriquí Grande Highway, Continental Divide, 1,200 m, *Croat & Grayum 60339* (CM, MO); 1.1–1.2 km N of Continental Divide, *Croat 60363* (MO, PMA, RSA), *60446* (MO). CHIRIQUÍ: Fortuna Dam area, *Hammel 2080* (MO, PMA), *Mendoza 336* (MO, PMA); 1,100–1,200 m, 8°45′N, 82°18′W, *Croat 66592* (MO), *Croat 48738* (MO); 1,200–1,600 m, *Croat 48737* (MO), *Folsom et al. 5516* (MO), *8220* (MO, PMA), *5607* (B, MO,

VEN); 5.9–8.6 mi. beyond Los Planes de Hornito, 1,260–1,400 m, *Antonio 5022* (MO), *Croat 48732* (MO), *48777* (MO, US), *49851* (CM, MO), *49930* (B, K, MO, NY, SEL, W), *49942* (B, K, MO, NY, PMA, SEL), *Knapp 4962* (MO), *Knapp & Vodicka 5496* (B, MO); N of Gualaca, 22.7 mi. beyond bridge over Río Estí, 1,400 m, *Antonio 2773* (MO, PMA), *Croat 48674* (B, CAS, CM, COL, DUKE, F, K, MEXU, MO, NY, PMA, RSA, UC, US, VEN); Fortuna Lake–Chiriquí Grande, Fortuna Dam, 4.5–5 km N of dam over Fortuna Lake, 1,100–1,135, *Croat & Grayum 60072* (K, MO).

Anthurium purpureospathum Croat, Selbyana 5(3–4): 328. 1981. TYPE: Panama. Bocas del Toro: Changuinola–Almirante Railroad, Station Milla 7.5, 0–100 m, *Croat 38094* (holotype, MO 2388335; isotypes, B, BM, C, CAS, CM, CR, DUKE, F, GH, IBE, K, LE, M, MISSA, NY, P, PMA, QCA, RSA, S, SEL, US, VEN, W). Figures 263, 264.

Epiphytic, or terrestrial at higher elevations; stem ca. 2 cm diam.; roots dense, descending, brown to greenish, smooth to scurfy, moderately thick, somewhat elongate, 3–5 mm diam.; cataphylls coriaceous to subcoriaceous, narrowly lanceolate, 7–14(25) cm long, obtuse to acuminate at apex, yellowish green, weakly tinged with red, drying dark tan (B & K yellow 5/2.5), persisting semi-intact, eventually as a reticulum of fibers. *Leaves* erect to spreading; petioles 12–37(66) cm long, 4–10 mm diam., quadrangular to D-shaped, flattened to broadly and sharply sulcate adaxially, the margins raised, rounded to 1–3-ribbed abaxially, the surface pale-speckled; geniculum thicker and paler than petiole, 1–2.5 cm long; blades subcoriaceous to moderately coriaceous, oblong-oblanceolate to oblong-elliptic, shortly acuminate at apex (the acumen apiculate), obtuse to acute or attenuate at base, 27–74(94) cm long, 7.5–40 cm wide, broadest at or above the middle, the margins broadly undulate; upper surface matte to semi-glossy, dark green, lower surface glossy to weakly glossy, paler; midrib above obtusely angular-raised to convex at base, becoming narrowly raised toward the apex, below prominently higher than broad and 1-ribbed at base, gradually becoming convexly raised toward the apex, paler than surface above and below; primary lateral veins (6)11–16 per side, departing midrib at 45–70° angle, arcuate-ascending, loop-connecting in the upper half of the blade, convexly raised in grooves, paler than surface above, prominently and convexly raised and somewhat darker than surface below; interprimary veins sometimes present, almost as conspicuous as primary lateral veins; tertiary veins weakly visible above, flat to weakly raised and darker than surface below; collective vein arising from about the middle or the base of the blade, weakly sunken above, raised and darker than surface below, less prominent than primary lateral veins, 4–8(13) mm from margin. *Inflorescences* erect to spreading; peduncle 3–38(50) cm long, 6–20 mm diam., rarely shorter than, mostly equaling or slightly longer than petiole, purplish or green, subterete; spathe subcoriaceous, purple to purplish with green mottling especially near the base at the center, oblong to narrowly ovate, 4.5–17.5 cm long, 1.5–4 cm wide, broadest just above the base, acute at apex (the acumen cuspidate), obtuse to rounded at base; spadix dark violet-purple (B & K purple 2/7.5), cylindroid to slightly tapered, (4)5–22 cm long, 3–10 mm diam. near base, 2–5 mm diam. near apex; flowers rhombic to weakly 4-lobed, 2–2.3 mm long, 2.5–3 mm wide, the sides smoothly to jaggedly sigmoid; ca. 14 flowers visible in principal spiral, ca. 7 in alternate spiral; tepals matte with small, scattered droplets; lateral tepals 1.4–1.6 mm wide, the inner margins flat against pistil; pistils slightly raised, purple becoming green and finally orange; stigma linear, ca. 0.5 mm long, droplets persisting for 4–10 days, drying with exserted papillae 4–6 days before stamens emerge; stamens emerging slowly from the base, held tightly in a circle around pistil; filaments transparent, flattened, soon retracting, holding anthers at level of tepals, 0.7–1 mm long, ca. 0.7 mm wide; anthers pale orange; thecae ellipsoid, usually not divaricate; pollen golden yellow (B & K yellow 8/2.5) fading to creamy white. *Infructescence* erect to spreading; spathe usually persisting; spadix 9–19 cm long, to 4 cm diam.; berries orange, red-orange to red (B & K red 6/7.5), narrowly ovoid, acute with minute, mammilliform style at apex, to 10 mm long; mesocarp pasty, transparent; seeds 1 or 2 per berry, pale greenish yellow, ca. 4 mm long, 2 mm diam.

This species is known only from Panama and occurs principally from near sea level to 1,500 m in Bocas del Toro and Chiriquí provinces in wetter parts of tropical moist and premontane wet forest. A collection from San Blas (*de Nevers 4207*) is out of range, but does not differ significantly from other collections from western Panama.

Anthurium purpureospathum is distinguished by its rosulate habit, large, thin, semi-intact cataphylls, more or less oblanceolate leaf blades, almost quadrangular petioles which are often three-ribbed abaxially, its generally short peduncles, usually violet-purple, reflexed spathe, usually short violet purple spadix, early-emergent pistils, and by

its long, sharply pointed, orange to red-orange berries.

This species is most closely related to *A. upalaense*, which differs in having leaves with the collective vein arising from above the middle of the blade, a generally longer peduncle, and a more long-tapered spadix.

An odd collection is *McPherson 8572*, because of its very large size. This collection counts for the parenthetical measurements for cataphyll, petiole, blade, and peduncle lengths in the description.

PANAMA. BOCAS DEL TORO: 15 km S of Changuinola, 300–500 m, *Antonio 3148* (MO); Ojo del Agua, 7 km W of Almirante, 190–220 m, *Croat 38179, 38180* (MO); Milla 7.5, hill above station, 30 m, *Croat & Porter 16416* (MO); 100 m, *Croat 38094* (B, BM, C, CAS, CM, CR, DUKE, F, GH, IBE, K, LE, M, MISSA, MO, NY, P, PMA, QCA, RSA, S, SEL, US, VEN, W); 10 mi. NW of Almirante, 0–100 m, *D'Arcy 11207* (MO); Almirante–Ojo del Agua, 3–6 km W of Almirante, 30–200 m, *Croat 38214* (MO, PMA); Chiriquí Lagoon, Shepherd Island, *von Wedel 2721* (GH, MO); Fortuna Road, Chiriquí Grande–Fortuna, 13.2 mi. W of Chiriquí Grande, 310 m, *Croat & Grayum 60145* (B, MO); 10 mi. from Continental Divide, 120 m, 8°55′N, 82°10′W, *McPherson 8572* (MO); 175 m, *Croat 66820* (MO); Isla Bastimentos. 1–2 km N of Trouble Hole, 30–100 m, *Peterson & Annable 6855* (US); Isla Colón, 0–120 m, *von Wedel 125* (MO), *569* (GH, MO); Río Changuinola, 1 mi. S of Changuinola, *Lazor & Tyson 2661* (MO); Río Cricamola, Finca St. Louis–Konkintoe, 10–50 m, *Woodson et al. 1889* (MO, NY); Río Guarumo, 5 mi. S of Chiriquicito, *Lewis et al. 1985* (MO, NY); Water Valley, *von Wedel 708* (MO), *774* (GH, MO). CHIRIQUÍ: Cerro Colorado, along mining road 24 mi. above bridge over Río San Félix, N of village San Félix, 1,430–1,500 m, *Croat 48483* (MO); along mining road 18–27 mi. off of Pan-Am Hwy., above Chamí or turnoff to Escopeta, above San Félix, 1,200–1,500 m, *Croat 33139* (CM, MO, NY); Bocas Road, 1,500 m, *Folsom & Collins 1835* (MO); 28 mi. above San Félix, 9–10 mi. above turnoff to Escopeta, 1,200–1,500 m, *Croat 33257* (MO, PMA); Fortuna Road, Chiriquí Grande–Fortuna, 7.7 mi. W of Chiriquí Grande, 1.5 mi. W of Punta Peña, 80 m, *Croat & Grayum 60090* (MO). SAN BLAS: El Llano–Cartí Road, Nusgandí, 19.1 km from Interamerican Hwy., 350 m, *de Nevers 4207* (MO).

Anthurium ranchoanum Engl., Bot. Jahrb. Syst. 25: 421. 1898. TYPE: Costa Rica. Heredia: Rancho Flores in territorio Bacha, Volcán Barba, 2,100 m, *Pittier 2295* (holotype, B; isotypes, BR, G). Figures 262, 265, 266.

Anthurium valerii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 137. 1937. TYPE: Costa Rica. Heredia: Vara Blanca, *Valerio 1600* (holotype, F).

Anthurium vinicolor Standley & L. O. Williams, Ceiba 3: 106. 1952. TYPE: Costa Rica. San José: Cordillera de Talamanca near Copey, 1,800 m, *L. O. Williams 16538* (holotype, EAP; isotypes, F, US).

Epiphytic or terrestrial; stem to 100 cm long, ca. 1.5–2 cm diam.; leaf scars occasionally conspicuous, 0.7–1 cm high, 1.5–1.7 cm wide; roots moderately numerous, descending, greenish, pubescent, sometimes smooth, moderately thick and elongate, blunt, 3–7 mm diam.; cataphylls subcoriaceous, 6–30 cm long, subrounded at apex with subapical apiculum, green tinged with red, drying tan (B & K yellow-red 9/2.5), persisting semi-intact, eventually deciduous. *Leaves* spreading; petioles 11–150 cm long, 5–15 mm diam., erect-spreading, subterete to nearly D-shaped, shallowly and narrowly sulcate to flattened adaxially, rounded abaxially, the surface faintly pale-speckled; geniculum slightly thicker and paler than petiole, 1.5–3 cm long; blades moderately coriaceous, somewhat pliable, narrowly ovate to ovate-deltoid to ovate-triangular, acuminate at apex (the acumen apiculate), shallowly or deeply lobed at base, 17–64 cm long, 9–34 cm wide, broadest between the base and middle, the margins undulate; anterior lobe 12–29 cm long, the posterior lobes 7–13 cm long; sinus arcuate to parabolic; both surfaces semiglossy to glossy, medium to dark green above, much paler below; midrib bluntly angular to convexly raised above (rarely acutely angular), much paler than surface, round-raised at base, becoming prominently and convexly raised toward the apex, paler than surface below; basal veins 3–6 pairs, 1st usually free to base, 3rd to 6th coalesced 1–2 cm, 4th to 6th coalesced 3.5–6 cm, raised above and below; posterior rib naked, turned up on outer margin; primary lateral veins 4–9 per side, departing midrib at 40–50° angle, broadly arcuate, weakly raised above and below, more so below; interprimary veins flat above, weakly raised below, less conspicuous than primary lateral veins; tertiary veins weakly visible above and below; collective vein arising from one of the primary lateral veins, sometimes from the first basal vein, raised to weakly sunken above, raised below, 2–10 mm from margin. *Inflorescences* erect to erect-spreading, much shorter than leaves; peduncle 13–100 cm long, 5 mm diam., 0.6–0.7× as long as petiole, green to purplish, terete; spathe spreading, hooded over the spadix, recurled at apex, subcoriaceous, green to green tinged with purple to purple or maroon, lanceolate to narrowly ovate, 4–35 cm long, 2–6.5 cm wide, broadest near the base, acute and apiculate at apex (the acumen tightly inrolled), truncate at base; stipe 1.6 cm long in front, 1.3 cm long in back; spadix pink to red to dark violet-purple to maroon, weakly tapered, 3.5–19 cm long, 9–15 mm diam. near base, 6–9 mm diam. near apex; flowers rhombic, 2–3.2 mm long, 2.6–

3(5) mm wide, the sides jaggedly sigmoid; 5–10 flowers visible in principal spiral, 7–20 in alternate spiral; tepals matte, sparsely punctate, moderately papillate; lateral tepals 1–1.8 mm wide, difficult to discern, the inner margins broadly rounded, the outer margins 3–4-sided; pistils not emergent, pale green; stigma slitlike, ca. 0.5 mm long; stamens emerging promptly throughout in a scattered pattern, becoming prominently exserted, lateral stamens emerging almost to apex before alternates emerge, surmounting tepals; filaments fleshy, somewhat flattened, translucent, ca. 0.5 mm long, ca. 1 mm wide; anthers creamy white to pale orange, ca. 0.6 mm long, 0.7 mm wide; thecae ovoid-ellipsoid, slightly divaricate; pollen yellow to yellow-orange, fading to white, yeasty-scented. *Infructescence* arching-pendent; spathe persisting; spadix to 50 cm long, to 3 cm diam.; berries orange, narrowly obovoid, acute at apex, 12–14 mm long, 6 mm diam.; mesocarp bitter; seeds 1–2 per berry.

Anthurium ranchoanum is found in Costa Rica and Panama at 500 to 2,300 m (usually above 1,000 m), usually in tropical wet, premontane rain and lower montane rain forest life zones.

This species is an atypical member of sect. *Pachyneurium*, recognized by its obtusely sulcate petioles and thick, ovate to ovate-triangular blades with heavy, rather numerous veins. Particularly characteristic is the ovate to lanceolate, hooded spathe which is green tinged with purple and remains stiffly erect. Other distinguishing features include the dark violet-purple, relatively stubby, scarcely tapered, somewhat pendent spadix with tight clusters of white stamens, and the orange berries.

Anthurium ranchoanum is most closely related to *A. cotobrusii*, which differs in having an erect, non-hooding spathe and a markedly tapered spadix which is 10–20× (vs. less than 6×) longer than thick.

Two collections worthy of mention are *Grayum & Dickie 6587* and *6590* which differ from typical collections in having blades drying thinner with less conspicuous tertiary veins, an acute midrib on upper surface and proportionally longer spadix at anthesis. They are perhaps subspecifically distinct.

COSTA RICA. ALAJUELA: Río La Paz Grande, 7.5 km N of Vara Blanca, 1,270–1,350 m, *Croat 36052* (MO); Sucre–Laguna Pozo Verde, toward Cerro Porvenir, 2,000 m, *Luteyn et al. 4502* (MO). CARTAGO: Copé, *Williams & Allen 16538* (US); ridge N of Continental Divide, E of Quebrada Siberia, ca. 2 km E of Villa Mills, *Grayum & Dickie 6587* (CM, CR, MO), *6590* (CR, MO). HEREDIA: Vara Blanca–Puerto Viejo, 5.5 km N of Vara Blanca, 1,200 m, *Croat 36053* (MO); headwaters of Río Santo Domingo, 3 km NE of San Rafael de Vara Blanca, N slope Volcán Barva, 2,060 m, 10°1.5′N, 84°07′W, *Grayum 7226* (MO); 1 km NE of Los Cartagos, 2,100 m, *Lent 1898* (MO); Cerro Chompipe–SW flank of Volcán Barva, N of Hwy. 113 connecting with Calle Gallito, 2,000–2,100 m, 10°7′N, 84°5′W, *Baker et al. 239* (MO); Monte Cristo, 1,720 m, *Rojas 511* (MO); slopes of Volcán Barva, above San Rafael and Uvita, along Río Segundo, 1,900–2,000, 10°05′N, 84°05′W, *Berringer & Schatz 2039* (MO); Parque Nacional Braulio Carrillo, San Rafael de Vara–Blanca, 1,830 m, 10°11′50″N, 84°6′35″W, *Herrera 242* (MO), *244* (MO); 1,800 m, *266* (MO); 2,000 m, *228* (MO); NNW of Heredia, *Lellinger & White 981, 1012* (US); road to Sacramento, *Utley & Utley 4564* (DUKE); San Isidro, *Pittier 14058* (US), *Standley & Valerio 50243, 50798, 51455, 51620, 52345* (US); N of San Rafael, *Lems s.n.* (K, NY); Braulio Carrillo Park, Zurquí, 1,700–2,000 m, *Gomez 20103, 20221* (CR, MO), *20225* (B, CR, F, K, MO); Cerro Caricias and Cerro Zurquí, S slopes, bordering Quebrada Caricias, NE of Heredia, 1,600–1,800 m, *Luteyn 3275* (MO); Cerro Chompipe, *Luteyn & Wilbur 4422* (DUKE); N slope, San Rafael–Río Las Vueltas, 2,100–2,200 m, 10°5′N, 84°4′W, *Stevens 13980* (MO); Río Vueltas, upper Río Patria, E slopes of Volcán Barva, Continental Divide, 2,000 m, 10°6′N, 84°4′W, *Burger & Liesner 6369* (MO); Volcan Barva, *Pittier 2295* (BR), *Skutch 3657* (MICH, US). PUNTARENAS: Cantón de Coto Brus, cultivated at Las Cruces Tropical Botanical Garden, 1,200 m, *Croat 44443, 57242* (MO); Monteverde, Río Guacimal, below Lechería, 1,500 m, 10°17′N, 84°48′W, *Hammel & Trainer 13816* (MO); near E edge of Monteverde Reserve, 1,350 m, *Croat 47130* (MO); 1,450 m, *Haber 4071, 4086, 4087* (MO); Río San Luis, 1,000 m, *Haber et al. 4975, 5016* (MO). SAN JOSÉ: N of San Isidro del General, *Utley 407* (DUKE); 5 km SW of Empalme on road to Santa María de Dota, 2,000 m, *Antonio 721* (MO); S of Santa María de Dota, *Luteyn 3324* (DUKE), *Standley 41767* (US), *Standley & Valerio 44077* (US); Santa Rosa del Copey, *Tonduz 12266, 12267, 12269* (US); Rio Cascajal, 3 km NE of Cascajal, 1,680 m, *Lent 2181* (MO). PANAMA. BOCAS DEL TORO: Cerro Colorado, along road between Río San Felix and mining exploration camp, 7 mi. W of Chamí, along trail through Guaymi village, 1,500 m, *Croat 69211* (MO); Cerro Pate Macho, NW ridge, from summit to Finca Serrano, 1,200–2,100 m, *Sytsma et al. 4949* (MO). BOCAS DEL TORO & CHIRIQUÍ: ridge of Continental Divide, NE of Cerro Pate Alto, 2,200 m, 8°47′N, 82°21′W, *Knapp & Schmalzel 4755* (MO). CHIRIQUÍ: Cerro Horqueta, Cordillera de Talamanca, above Boquete, 1,860–1,940 m, 8°49′N, 82°29′W, *Cochrane et al. 6264* (MO); NW of Boquete, 1,660–1,930 m, *Herrera 545* (MO); Cerro Hornito, 1,400–1,750 m, *Folsom et al. 7224* (MO); 1,750–1,900 m, 8°41′N, 82°10′W *Croat 67985* (MO); Cerro Hornito summit, above Los Planes de Hornito, 2,100–2,230 m, *Hammel 6217* (MO), *Knapp et al. 4202* (MO); Cerro Horqueta, *Dwyer et al. 545* (GH, MO, US); Cerro Pando, E slopes, 2,000–2,300 m, 8°55′N, 82°44′W, *Knapp 1653* (K, MO); Cerro Pate Macho, Continental Divide, NE of Cerro Pate Macho, Bocas del Toro border, above Palo Alto, 2,200 m, 8°47′N, 82°21′W, *Knapp et al. 4240* (MO); along Continental Divide, NE of Boquete, 1,800–2,200 m, *Croat 48519A* (CM, MO), *Croat 48553* (MO), *Croat 66407* (MO); Cerro Punta, 2.7 mi. NW of Río Chiriquí Viejo, Las Nubes, 2,200 m,

Liesner 326 (MO, PMA); Fortuna Road, 1,300 m, *McPherson 8779* (B, MO, NY, PMA); Fortuna Dam, ridge 7 mi. N of Los Planes de Hornito, 1,000 m, *Knapp et al. 4177* (MO); Gualaca–Fortuna Dam, 5.9 mi. NW of Los Planes de Hornito, 1,370 m, *Croat 49846* (MO); Fortuna Dam, 1,200–1,400 m, *Hammel 2113* (MO); Río Palo Alto headwaters, 0.5 km E of Cerro Pate Macho, 1,800–2,100 m, 8°47′N, 82°21′W, *Knapp et al. 2120* (MO); Dtto. Bugaba, Cerro Pando, Santa Clara, 8°50′N, 82°44′W, *van der Werff & Herrera 7275* (MO, PMA, RSA).

Anthurium reflexinervium Croat, sp. nov. TYPE: Peru. Huánuco: Prov. Leoncio Prado, Dtto. Rupa Rupa, Tingo María, vic. of airport, 750–800 m, *Plowman & Ramírez 7585* (holotype, MO 2743714; isotypes, F, K, NY, SEL). Figures 267, 268, 271.

Planta epilithica; internodia brevia, 1–3 cm diam.; cataphyllum late lanceolato-trigonum; petiolus 3–8 cm longus, (4)6–12 mm diam., trigonus, aliquando D-formatus; lamina late oblanceolato-elliptica, 41–72 cm longa, (10.5)13–18 cm lata; nervis primariis lateralibus 23–26(35) utroque, manifeste retrorse arcuati; pedunculus 18–40 cm longus, 3–6 mm diam.; spatha lanceolato-ovata aut oblongo-lanceolata aut oblongo-elliptica, 4.5–9 cm longa, 0.7–2.1 cm lata; stipes ad 5 mm liber; spadix contractus, 6–11 cm longus, basi 5–9 mm diam., apice 2–5 mm diam., rubellus-violaceus ad atrorubellum-purpureum. Baccae rubro-violaceae, 8 mm longae.

Epilithic; stem usually less than 15 cm long, 1–3 cm diam.; leaf scars 0.7 cm high, 1 cm wide; roots dense, ascending to descending, brown, smooth to tomentose, weakly tapered, 3–4 cm long, 3–5 mm diam.; cataphylls subcoriaceous, broadly lanceolate-triangular, (2)4–4.5 cm long, acute at apex, drying dull brown, persisting semi-intact, quickly dilacerating and persisting as fine linear fibers, splitting at apex. *Leaves* erect to spreading; petioles 3–8 cm long, (4)6–12 mm diam., broadly and sharply triangular, sometimes sharply D-shaped, flattened, sometimes with a medial rib adaxially, the margins winged and undulate, prominently and sharply angular to rounded abaxially; geniculum scarcely to moderately thicker than petiole, 0.5–1 cm long; sheath 2–3.5 cm long; blades coriaceous to subcoriaceous, broadly oblanceolate-elliptic, acute at apex, obtuse to shallowly cordate at base, 41–72 cm long, (10.5)13–18 cm wide, broadest at or above the middle, the margins sometimes concave toward the base, moderately to strongly undulate; upper surface matte to semiglossy, dark green, lower surface semiglossy, paler; both surfaces strongly bullate and quilted; midrib flat and with a sharp rib at base, becoming acutely raised and higher than broad toward the apex above, acutely raised, higher than broad and 1-ribbed to winged below; primary lateral veins 22–26(35) per side, departing midrib at acute to obtuse angle, spreading retrorsely at 30–70° angle, conspicuously arcuate to the collective vein, narrowly raised in deep grooves above, less so below, knife-edge-like when dried below, less so above; interprimary veins few, almost as conspicuous as primary lateral veins; tertiary veins weakly raised to flat below, weakly visible above and below when dried; reticulate veins obscure to conspicuous when dried, flat; collective vein arising from near the apex, about the middle of the blade or near the base, equally as prominent as major tertiary veins, 2–5 mm from margin. *Inflorescences* erect; peduncle 15–40 cm long, 3–7 mm diam., 2.8–8(11)× as long as petiole, olive-green to dark green, terete with a diminishing rib, firm; spathe ascending to reflexed, sometimes recurled, subcoriaceous to coriaceous, olive-green to pale olive-green, tinged with red to uniformly dark green, lanceolate-ovate to oblong-lanceolate to oblong-elliptic, 4.5–9 cm long, 0.7–2.4 cm wide, broadest near the base, inserted at 45–80° angle on peduncle, abruptly acuminate at apex (the acumen tightly inrolled and cuspidate, 2–3 mm long), narrowly acute to obtuse to rounded at base, the margins meeting at 80° angle; stipe ca. 6–13(20) mm long in front, 1–6 mm long in back; spadix red-violet to dark red-purple (B & K purple 4/7.5), tapered, erect, somewhat curved, 6–11 cm long, 5–10 mm diam. near base, 2–5 mm diam. near apex, broadest at the base; flowers ± square, 2.0–2.5 mm long when fresh, drying 1.9–2.4 mm long, 2.5–3.7 mm wide when fresh, drying 1.7–1.9 mm wide, the sides straight to smoothly or jaggedly sigmoid; 5–9 flowers visible in principal spiral, 4–14 in alternate spiral; tepals densely and minutely papillate; lateral tepals 1.1–2 mm wide, the inner margins ± straight to broadly convex, weakly erose, the outer margins 2–3-sided; pistils weakly raised, greenish, somewhat papillate; stigma slitlike, becoming broadly ellipsoid to nearly circular, 0.4–0.5 mm long, depressed medially with the margins somewhat raised when fresh, drying slightly sunken and blackish; stamens emerging rapidly in a complete sequence, the laterals preceding the alternates by 6–14 spirals, 3rd preceding 4th by 1–2 spirals, held at the sides of the pistil; anthers yellow, 0.5–0.9 mm long, 0.7–1.0 mm wide; thecae ovoid-ellipsoid, not divaricate. *Infructescence* with spathe green, persisting; berries reddish violet, 8 mm long.

Anthurium reflexinervium is known only from the vicinity of Tingo María in Huánuco, Peru, at 650 to 800 m, on rocky slopes near the Río Huallaga, in a premontane tropical moist–tropical moist forest transitional life zone.

This species is easily recognized by its strongly quilted-bullate leaf blades with numerous, prominently retrorse, arcuate primary lateral veins (hence the name). Prominently retrorse primary lateral veins are otherwise found only in *A. latissimum* and *A. paraguayense* var. *coroicoanum*, but these lack strongly bullate leaf blades and have retrorse veins only toward the base. Other species may occasionally have a few retrorse primary lateral veins near the base.

Anthurium reflexinervium is a stunning horticultural subject, at present cultivated at several botanical gardens and in a few private collections.

PERU. HUÁNUCO: Tingo María Region, Tingo María–Monzón, Río Patay Rondos, Cuevas de Guácharo, 650 m, 9°21'S, 76°12'W, *Croat 57949* (BM, CAS, CM, MO, NY, RSA, SEL, U, US, USM); Río Huallaga, *Croat 21080* (MO); Prov. Leoncio Prado, Río Huallaga, near airport, 700–800 m, *Plowman 5823A* (GH); Prov. Leoncio Prado, Dtto. Rupa Rupa, Tingo María, 750–800 m, *Plowman & Ramírez 7585* (F, K, MO, NY, SEL).

Anthurium remotigeniculatum Croat, sp. nov. TYPE: Peru. San Martín: along road between Tarapoto and Yurimaguas, 530 m, *Croat 58114* (holotype, MO 3183169; isotypes, B, GH, K, M, NY, QCA, RSA, SEL, US, USM). Figures 272, 275.

Planta terrestris, aliquando epilithica; internodia brevia, 1.5–6 cm diam.; cataphyllum anguste trigonum; petiolus 10–34 cm longus, 5–10 mm diam., D-formatus; geniculum ad 16 cm remotum; lamina ovata ad obovata vel late elliptica, (20)27–100 cm longa, (9)14–28.5 cm lata; nervis primariis lateralibus 6–8 utroque; pedunculus 63.5–96 cm longus, 7–17 mm diam.; spatha linearis-lanceolata, 10.5–12 cm longa, 0.5–1.5 cm lata, viridis; stipes usque ad 4 mm liber; spadix longus et graduatim contractus, 10.5–25 cm longus, basi 6–7 mm diam., apice 3–4 mm diam., atroviolaceo-purpureus; baccae rubello-purpureae, ca. 5.8–6 mm longae, 2.8–3.7 mm diam.

Terrestrial, occasionally epilithic; stem short, 1.5–6 cm diam.; roots few, descending, greenish to brown, smooth to densely pubescent, elongate, 4–6 mm diam.; cataphylls coriaceous to subcoriaceous, narrowly triangular to broadly lanceolate, unribbed, 3–7.5 cm long, acute at apex, reddish purple, drying brown (B & K yellow 3/2.5), persisting intact, eventually deciduous. *Leaves* erect to erect-spreading; petioles 10–34 cm long, 5–10 mm diam., D-shaped, narrowly and obtusely sulcate adaxially with the margins blunt, not raised, rounded abaxially, the surface pale-speckled; geniculum thicker, slightly paler than, and more shallowly sulcate than petiole, becoming fissured transversely with age, 1.5–2 cm long, remote from the base of the blade ca. 2–16 cm, rarely contiguous; blades coriaceous, ovate to obovate to broadly elliptic, abruptly acuminate, sometimes acute at apex (the acumen weakly apiculate and downturned), long-attenuate at base, (20)27–100 cm long, (9)14–28.5 cm wide, broadest at or above the middle, the margins weakly to prominently undulate; upper surface matte to weakly glossy, medium to dark green, lower surface matte, conspicuously to moderately paler, appearing minutely pale-speckled and with translucent, alveolate pattern on high magnification when fresh; both surfaces drying yellowish to yellowish green; midrib above flat to convexly raised at base, becoming more convex toward the apex and paler than surface, below prominently higher than broad at base, becoming convexly raised toward the apex and slightly paler than surface; primary lateral veins 6–8 per side, departing midrib at 30–60° angle, straight near the midrib, becoming arcuate-ascending near the margin, weakly convexly raised and scarcely paler than surface above, prominently raised below, drying prominently raised above and below; interprimary veins weakly visible and sunken above, slightly darker than surface, scarcely raised below; tertiary veins sunken above, weakly raised and darker than surface below; collective vein arising from about the middle of the blade or in the upper third, slightly sunken above, raised and darker than surface below, 5–15 mm from margin. *Inflorescences* erect to spreading, equaling or longer than leaves; peduncle 63.5–96 cm long, 7–17 mm diam., 2–4× as long as petiole, green to green heavily tinged with purple; spathe spreading-recurled, coriaceous to subcoriaceous, plain green or heavily to slightly tinged with purple, linear-lanceolate, 10.5–13.5 cm long, 0.5–3 cm wide, broadest near base, acute at apex (the acumen inrolled), acute to decurrent at base; stipe 1.3–2.5 cm long in front, to 4 mm long in back; spadix maroon to dark violet-purple (B & K purple 2/2.5), long-tapered, curved, 10.2–25 cm long, 6–8 mm diam. near base, 3–4 mm diam. near apex; flowers ± square, 1.8–2.5 mm in both directions, the sides straight to smoothly sigmoid; 4–8 flowers visible in principal spiral, 7–13 in alternate spiral; tepals matte, densely and minutely papillate, scarcely punctate; lateral tepals 0.9–1.8 mm wide, the inner margins convex, the outer margins irregularly 2–3-sided; pistils emergent, densely and minutely papillate, reddish purple, becoming green; stigma linear, slitlike, 0.5–0.7 mm long; the lateral stamens preceding the alternates by 3–4 spirals, the 3rd stamen preceding the 4th by 3–5 spirals, held in a tight cluster above the pistil; anthers yellow, 0.4–0.6 mm long, 0.8–1 mm wide, scarcely exserted; thecae ovoid, slight-

ly or not divaricate; pollen yellow fading to white. *Infructescence* with spathe absent; spadix at least 13 cm long, 1.5 cm diam.; berries obovoid, reddish purple, white at base, rounded at apex (truncate when dried), ca. 6.5–7.5 mm long, 5–6 mm diam., mesocarp juicy, translucent; seeds 2, 4.5–5.0 mm long, 2.5 mm diam., scarcely flattened, reddish purple, minutely pale-speckled.

Anthurium remotigeniculatum is recorded only from Peru, where it occurs in the provinces of San Martín and Amazonas at 530 to 1,160 m, in tropical moist and tropical premontane wet forest life zones.

This species is characterized by its terrestrial habit, short cataphylls that remain semi-intact, D-shaped petioles which are obtusely and bluntly sulcate adaxially, and its elongate, long-tapered, dark purple spadix. Especially significant is the leaf blade base, which is long-attenuate (especially in older plants) and eventually naked, making the geniculum seem remote sometimes for as much as 16 cm from the base of the blade, hence the specific epithet. Also characteristic are the coriaceous leaf blades which are ovate, obovate, or broadly elliptic, dark green above and conspicuously paler below, appearing speckled and with a translucent, alveolate pattern under high magnification on fresh plants.

Anthurium remotigeniculatum is most closely allied to *A. pachylaminum*, which differs in having more coriaceous leaf blades lacking the remote geniculum.

Although most of the specimens of *A. remotigeniculatum* display the remote geniculum characteristic very clearly, there are some exceptions. Specimens lacking this feature otherwise show remarkable similarity to more typical material. Observations on living material show that the same plant may produce the characteristic leaves with a remote geniculum and "normal" leaves at the same time, and such aberrant specimens have thus been included in the species concept.

PERU. AMAZONAS: Prov. Bagua, 15.6 km E of main plaza in Bagua, 5 km above La Peca, 1,051–1,160 m, 5°33′S, 78°21′W, *Croat 58360* (B, BM, F, GH, K, M, MBM, MO, NY, P, QCA, SEL, US, USM, W). SAN MARTÍN: Tarapoto–Yurimaguas, 1,200 m, cultivated at SEL (#81-2283) (MO); Dtto. Tarapoto, Tarapoto–Yurimaguas, Km 13, 750–1,000 m, *Rimachi 5781* (IBE); Km 12–13.5, 700 m, *Rimachi 5173* (IBE); Río Huallaga, Tarapoto–Yurimaguas, 530 m, 6°30′S, 76°21′W, *Croat 58114* (B, K, GH, M, MO, NY, QCA, RSA, SEL, TEX, US, USM).

Anthurium salvadorense Croat, Selbyana 5(3–4): 333. 1981. TYPE: El Salvador. Ahuachapán: 1.5 mi. SW of Tacuba on road to San Francisco Menéndez, riverbank of Río Chokama, 700 m, *Croat 42169* (holotype, MO 2583750; isotypes, CAS, F, ITIC, K, LE, M, MEXU, RSA, SEL, TEX, US). Figures 269, 273.

Terrestrial or epilithic; stem short, 2–5 cm diam.; roots numerous, dense, descending to spreading or ascending, pale green to tinged reddish, smooth to pubescent, short and moderately thick, bluntly pointed at apex, 4–10 mm diam.; cataphylls moderately coriaceous, shortly lanceolate, 5–12.5 cm long, pale yellowish green, acute and apiculate at apex, drying light to dark brown, persisting partially intact, eventually deciduous. *Leaves* erect to spreading; petioles 9.5–46 cm long, (4)6–10 mm diam., ± quadrangular to D-shaped, broadly and shallowly to deeply sulcate, sometimes with medial rib adaxially, the margins blunt to sharp and raised, rounded to multi-ribbed abaxially, the surface pale-speckled; geniculum thicker than petiole and paler than petiole, 1–2 cm long; blades subcoriaceous, elliptic to broadly elliptic to oblanceolate, gradually to abruptly acuminate at apex (the acumen downturned, ca. 15 mm long), acute to obtuse to narrowly rounded at base, 25–65 cm long, 8–26 cm wide, broadest at or above middle, the margins undulate; upper surface matte to semiglossy, lower surface matte; medium green above, slightly paler below; midrib above flat with weak medial ridge at base, becoming obtusely angular and eventually sunken toward apex, below higher than broad, 1–4-ribbed at base, becoming prominently and convexly raised or convexly raised with a rib toward the apex and slightly paler than surface; primary lateral veins 7–14 per side, departing midrib at 45–60° angle, straight, loop-connected in the upper half, convexly raised above and below, slightly paler than surface; interprimary veins few, raised above and below; tertiary veins sunken to flat above, raised below; collective vein arising from about the middle of the blade or higher, sunken above, raised below, 5–12 mm from margin. *Inflorescences* erect to spreading; peduncle 13–57 cm long, 3–7 mm diam., 1.4–2.8× as long as petiole, light green, terete, weakly multi-ribbed; spathe erect to spreading, becoming recurled, moderately coriaceous, pale yellow-green (B & K yellow-green 8/10), ovate-lanceolate to oblong-lanceolate, 4.5–10 cm long, 1–4.3 cm wide, broadest just above the base, inserted at 155–170° angle on peduncle, acuminate at apex (the acumen apiculate and inrolled), subcordate and decurrent on peduncle at base; spadix pale green (B & K green 8/5), sessile, cylindroid

to weakly tapered, somewhat curved, 2.5–11 cm long, 7–12 mm diam. near base, 4–7 mm diam. near apex; flowers ± irregularly 4-lobed, 2–3.3 mm long, 2.5–3.6 mm wide, the sides prominently jaggedly sigmoid; 6–8(10) flowers visible in principal spiral, 9–12 in alternate spiral; tepals smooth, matte; lateral tepals 1.4–1.7 mm wide, the inner margins rounded, somewhat erose, sometimes turned up against pistil, the outer margins irregularly 2–4-sided; pistils weakly emergent, prominently raised before stamens emerge, dark green; stigma circular to ellipsoid, 0.3–0.4 mm long, erect and brushlike, droplets appearing 2–4 days before stamens emerge, stamens emerging rapidly in a complete sequence from the base, lateral stamens almost to apex before stamens emerge; anthers pale green, 0.8–1.2 mm long, 0.7–1.3 mm wide, contiguous, inclined over pistil; thecae weakly divaricate; pollen pale yellow, soon fading to white, sweetly fruit-scented. *Infructescence* spreading; spathe persisting and erect; spadix 6.5–10.5 cm long, ca. 2 cm diam.; berries orange-red (B & K yellow-red 5/2.5 to red 4/10), broadly obovoid, rounded to flat or weakly indented at apex, 5.5–9 mm long, 4–9 mm diam.; pericarp moderately thickened, with numerous punctiform raphide cells especially in the apical half; mesocarp pulpy or mealy, with numerous raphide cells; seeds 1 or 2, yellowish white to tan, obovoid to broadly obovoid, 6–6.5 mm long, 5–5.8 mm diam., 3 mm thick, densely covered with punctiform raphide cells.

Anthurium salvadorense is known only from El Salvador and Guatemala at 500 to 800 m. It was first collected by Sixto Alberto Padilla in 1922 in the Department of Ahuacapán in El Salvador. The species was later collected by Paul C. Standley in the adjacent Department of Jutiapa in Guatemala.

This species is a typical member of the section, and earlier collections were confused with *A. schlechtendalii*, to which it is related. *Anthurium salvadorense* differs in being a usually well-rooted plant with fewer, very large fleshy roots and a usually almost elliptic blade, but especially by its inflorescence, which has a pale green, ovate-lanceolate spathe that is weakly convolute at the base and erect, enshrouding the usually short, pale green spadix. *Anthurium schlechtendalii* differs in having usually oblanceolate blades, a coriaceous, more lanceolate, prominently reflexed, usually purplish spathe, and a more elongate, purplish spadix.

El Salvador. AHUACHAPÁN: San Francisco Menéndez–Tacuba, El Imposible, 500 m, *Bernhardt s.n.* (MO), *Croat 42092* (B, BM, MO, RSA, U, W); Río Chokama, 1.5 mi. S of Tacuba, 700 m, *Croat 42169* (CAS, F, ITIC, K, LE, M, MEXU, MO, RSA, SEL, TEX, US). Guatemala. JUTIAPA: Jutiapa, *Standley 76313* (F, US); SW of San Cristóbal, *Dunn et al. 23222* (UMO); Monjoy Canyon, 8 mi. W of San Cristóbal, 530 m, *Dunn et al. 19* (MO).

Anthurium salviniae Hemsley, Diagn. Pl. Nov. Mexic. 36. 1878. TYPE: Guatemala. Volcán de Fuego, *Salvin s.n.* (holotype, K). Figures 15, 20, 270, 274, 276.

Anthurium giganteum Matuda, Madroño 10: 169. 1950. non Engl. 1898. TYPE: Mexico. Chiapas: Escuintla, Salto de Agua, *Matuda 18043* (holotype, MEXU; isotype, UC).

Anthurium enormispadix Matuda, Revista Soc. Mex. Hist. Nat. 11: 94. Dec. 1950. TYPE: Same as *Anthurium giganteum* Matuda.

Epiphytic, rarely epilithic; stem to 6 cm diam.; roots dense, usually ascending, some descending, moderately numerous, greenish to white, pubescent, moderately short and tapered, 3–6 mm diam.; cataphylls thick, fistlike, cucullate, rounded at apex, drying brown, persisting intact, ultimately becoming fibrous at base. *Leaves* erect to spreading; petioles (3)5–23 cm long, 10–20 mm diam., ± D-shaped to terete, flattened to sulcate adaxially, the margins not prominent, rounded abaxially (once reported as prominently 5–7-ribbed), the surface pale-speckled; geniculum paler and thicker than petiole, 0.7–2 cm long; blades moderately coriaceous, obovate to oblanceolate to broadly elliptic, acuminate to obtuse at apex, attenuate to rounded or truncate (rare subcordate) at base, (32)39–180 cm long, (9)13–50 cm wide, broadest usually above (sometimes at or near the middle), the margins slightly undulate; both surfaces semiglossy, medium green (B & K yellow-green 4/7.5) above, slightly paler below; both surfaces drying greenish to brownish green; midrib convexly raised at base, becoming acute toward the apex above, convexly raised at base, becoming obtusely raised toward the apex below; primary lateral veins 9–24 per side, convexly raised above and below; interprimary veins rarely present; tertiary veins weakly raised to obscure above, weakly raised to flat and darker than surface below; collective vein arising from near the apex or absent (often from below the middle in small plants), weakly raised, 3–5 mm from margin. *Inflorescences* spreading to usually pendent, shorter than leaves; peduncle 16–80 cm long, 2–5 mm diam., 3.1–10.3× as long as petiole, terete; spathe spreading to recurled, coriaceous to subcoriaceous, purple or sometimes green tinged with red or purple (B & K yellow-green 6/5), lanceolate-linear, (4)10.5–40(50) cm long, 1–2.5 cm wide, inserted at 45–90° angle on peduncle,

gradually acuminate at apex (the acumen cuspidate, inrolled), rounded to truncate or acute at base; spadix pale green when immature, soon lavender to dull violet-purple to purple-maroon, glaucous, long-tapered, slightly curved, (6)10–34(47) cm long, 4–15 mm diam. near base, 2–7 mm diam. near apex; flowers rhombic, 2.4–2.5 mm in both directions, the sides straight to sigmoid; 6–8 flowers visible in principal spiral, 4–12 in alternate spiral; tepals matte; lateral tepals 1.2–1.3 mm wide, the inner margins broadly rounded; pistils emergent but not raised, green; stigma linear to oblong-elipsoid, 0.6–0.9 mm long; stamens emerging from the base in a slow, regular progression; anthers orange to pale yellow to creamy white, ca. 1 mm long, 0.9 mm wide, held at edge of tepals and inclined over pistil; thecae ellipsoid; pollen pale yellow-orange fading to white. *Infructescence* with spadix to 60 cm long; berries red, oblong-ellipsoid, rounded at apex, 10–15 mm long; mesocarp transparent, gelatinous; seeds 2 per berry, oblong, flattened, ca. 3–5 mm long.

Anthurium salviniae ranges from western Mexico (Chiapas), along the Pacific slope of Guatemala, and along the Atlantic and Pacific slopes from Nicaragua to Panama. There is also a single collection from Honduras (Atlantic slope) that appears to belong to this species. The species also occurs in Colombia, where it has been collected from Chigorodo and Dabeiba in Antioquia and Chocó departments. *Anthurium salviniae* occurs from near sea level to 1,600 m in wetter parts of tropical moist forest, in premontane wet, tropical wet, and also, rarely, in premontane rain forest.

This species is characterized by its cucullate cataphylls, large, mostly oblanceolate leaves with circinate vernation, usually pendant inflorescence with a slender peduncle and slender, long-tapered, pale lavender spadix and red berries.

Anthurium salviniae has long been called *A. tetragonum*, but that name is a synonym of *A. schlechtendalii*, a species ranging from Mexico to Honduras or Nicaragua on the Atlantic slope. Although leaves of the two species are very similar, *A. salviniae* can be distinguished by its long-tapered, pale lavender, glaucous spadix, long-tapered, spreading spathe, and by its fist-shaped, cucullate cataphylls. In addition, the leaves of *A. salviniae* usually dry darker and thinner. *Anthurium schlechtendalii* usually has a shorter, blunter spadix and a short, thick spathe that is usually reflexed and often twisted. The spadix is darker violet-purple, and is not at all glaucous at anthesis.

A collection in cultivation at the Missouri Botanical Garden from the Río Majé region of Panama, in Panamá Province, is unusual in having dark violet-purple rather than red berries.

COLOMBIA. ANTIOQUIA: Quebrada La Puerca–Malagon, 10 m, *Rentería et al. 4776* (MO); Río Claro, Pto. Triunfo–Medellín, S of Hwy., 5°54′N, 74°51′W, *Croat 56579* (MO); Río Sucio, Dabeiba, *Gutiérrez & Barkley 1822* (COL, US), *Johnson & Barkely 18C411* (US); Dabeiba–Chigorodó, 4 km NW of Dabeiba, 180–400 m, *Callejas et al. 4783* (MO); Mpo. Chigorodo, *Plowman 3175* (GH). CHOCÓ: Quebrada Resaquita, Mecana, 50 m, 6°16′N, 77°21′W, *Juncosa 1879* (MO). QUINDIO: Mpo. Montenegro, Río La Vieja, La María, 1,000 m, *Arbeláez et al. 333* (MO); Mpo. Turbo; Km 11 on Carretera Tapón del Darién, Leon–Lomas Aisladas area, 10–20 m, *Brand & Escobar 727* (MO). COSTA RICA. ALAJUELA: N of Zarcero, *Croat 43640* (MO); Naranjo–Quesada, Hwy. 15, 3.2 mi. N of Zapote, 1,560 m, *Croat 46916* (MO); Cañas–Upala Road, N of Bijagua, *Croat 36480* (COL, MO, NY); Río Cacao, 800 m, *Gómez 19568* (MO). Buena Vista de Zarcero, Finca Los Ensayos, 900–1,000 m, 10°16′N, 84°27′W, *Judziewicz 4404* (WIS). CARTAGO: SE of Platanillo, *Croat 36808* (MO); NE of Tapantí, *Lent 1034* (GH). GUANACASTE: Tilarán, *Standley & Valerio 44445* (US); Cerro Nubes, W slope, 2 km E of Silencio de Tilarán, 900 m, 10°28′N, 84°53′W, *Grayum et al. 4999* (MO); Lake Arenal, Río Chiquito–Río Caño Negro, 550–850 m, 10°27′N, 84°50′W, *Hammel et al. 15146* (MO); Parque Nacional Rincón de la Vieja, SE slopes of Volcán Santa María, above Estación Hacienda Santa María, 900–1,200 m, 10°47′N, 85°18′W, *Davidse et al. 23335* (CR, K, MO); on path from Puesta Santa María toward hot springs, *Garwood et al. 746b* (BM). PUNTARENAS: San Vito de Java, *Croat 32898* (MO); Cordillera de Talamanca, Río Guineal, Helechales, 1,100–1,200 m, 9°04′30″N, 85°05′W, *Davidse & Herrera 26240* (MO); Monteverde, Río Guacimál, Lechería, 1,500 m, 10°17′N, 84°48′W, *Hammel & Trainer 13830* (MO). GUATEMALA. ESCUINTLA: Escuintla–Sta. Lucía Cotz, *Standley 63469* (F). RETALHULEU: Ajaxa, *Standley 88227* (F); W of Retalhuleu, *Standley 87499, 88391* (F). SACATEPÉQUEZ: Las Lajas, *Standley 58294* (F). SAN MARCOS: La Trinidad, *Croat 40902* (CM, K, MEXU, MO, USCG), *40903* (MO). SANTA ROSA: Cuilapilla, *Standley 78060* (F); Naranjo, 1,200 m, *Hyde & Lux 4278* (G, K, NY, US). SUCHITEPÉQUEZ: E of Mazatenango, *Croat 32786* (MO). HONDURAS. ATLANTIDA: Lancetilla Valley, near Tela, *Standley 53228* (US). MEXICO. CHIAPAS: Escuintla, *Croat 43845, 43877* (MO), *Matuda s.n.* (MEXU), *16377* (F, MEXU, MO), *16776* (F, MEXU), *18043* (MEXU, UCLA), *18381* (DS, MEXU, PMA), *18519* (DS, MEXU, UCLA); Finca California–summit of Monte Ovando, *Croat 47572, 47573* (MO); Guatimoc, *Miranda 1763* (MEXU). NICARAGUA. JINOTEGA: Las Camelias–La Salvadora, rd. from Hwy. 3 through La Fundadora, 1,100–1,150 m, 13°05–06′N, 85°53–54′W, *Stevens & Grijalva 15326* (MO); La Palestrina–La Fundadora, rd. from Hwy. 3 through La Fundadora, 1,150–1,250 m, 13°03–04′N, 85°54′W, *Stevens & Grijalva 15325* (MO). MATAGALPA: Quebrada El Quebradón, Macizos de Peñas Blancas, WNW of Hacienda San Martín, 1,400–1,600 m, 13°15′N, 85°39′W, *Stevens et al. 21219* (MO). MATAGALPA–JINOTEGA: Quebrada El Quebradón, Macizos de Peñas Blancas, N of Hacienda San Martín, 950–1,400 m, 13°14–15′N, 85°39′W, *Stevens & Riviere 20892-b, 21035* (MO). RÍO

SAN JUAN: San Juan del Norte, *Smith 87* (MO). ZELAYA: Cerro El Inocente, S slope, *Stevens 6793* (MO). PANAMA. WITHOUT LOCALITY: *Duke 11427* (OS). CANAL AREA: Balboa, *Standley 28564* (MO); Gatún, hills W of Canal, *Standley 27210* (US); Culebra, *Gaillard 2698* (US); Frijoles, *Pittier 2679* (US); Gorgona–Gatún, *Pittier 2278* (US); Las Cascadas, *Dodge & Hunter 8651, 8659a, 8662* (MO); Obispo, *Standley 31719* (US); Salamanca Hydrographic Station, *Dodge et al. s.n.* (MO); Summit Gardens, *Croat 10281* (MO), *32983* (M, MICH, MO, RSA, TEX); Ancón Hill, Orchid Garden, *Bartlett & Lasser 16609* (MICH, MO); Barro Colorado Island, *Bailey & Bailey 72* (BH), *Croat 4231, 4554, 6511, 7292, 8495, 8512, 9534, 11325* (MO), *7920, 10195* (MO, PMA), *Ebinger 181* (MO), *Shattuck 638* (MO); Gatún Lake, *Standley 31343* (US); Madden Dam, Azote Caballo Road, *Dodge 16579* (MO); Quebrada Ancha, *Steyermark & Allen s.n.* (MO); Río Casaya headwaters, E of Gamboa, *Nee 9024* (MO); Río Indio de Gatún, *Pittier 2801* (US). CHIRIQUÍ: SW of Portobelo, *Liesner 1075* (MO, US); mining rd. above San Félix, 18–27 mi. off Panamerican Hwy. (above Chamí), 1,200–1,500 m, *Croat 33085* (B, C, K, MBM, MO, US); Cerro Colorado, *Antonio 1527* (MO), *Croat 33498* (MO, UCLA); Puerto Armuelles region, W of Puerto Armuelles, San Bartolo Limite, *Busey 593* (MO). COLÓN: Portobelo Region, Río Guanche, 1–4 km S of Portobelo hwy., 0–50 m, 9°30′N, 79°40′W, *Knapp & Schmalzel 3598* (MO), *Knapp et al. 4609* (MO); Río Boquerón, E of Salamanca, 50 m, 9°35′N, 79°32′W, *Knapp et al. 5826* (MO, B). DARIÉN: line CC, *Duke 5235* (MO); NE of Jaqué, *Sytsma & D'Arcy 3433* (K, MO); Cerro Sapo, Río San Antonio at base of cerro, 5 km S of Garachiné, 130 m, 7°59′N, 78°25′W, *Hammel et al. 14802* (MO), *14811* (M, MO); Cerro Tacarcuna, S slope, *Gentry & Mori 13892* (MO); Serranía de Pirre, *Croat 37751* (MO). PANAMÁ: S of Alcalde Díaz, *Nee 8566* (MO); Alajuela, *Pittier 2344* (US); Tortí Arriba, *Folsom et al. 6584* (MO); Cerro Brewster, SW of mountain, *Lewis et al. 3475* (MO); Río Majé, *Croat 34441* (MO), *34600* (F, K, MO, US); Serranía de Majé, *Folsom & Collins 1701* (MO); confluence of Río Ambroino and Río Ipeti, 100 m, 8°57′N, 79°32′W, *Churchill & de Nevers 4479* (MO); Parque Nacional del Darién, ridge between Río Topalisa and Río Pucuro, ca. 13 km E of Pucuro, 8°03′N, 77°20′W, 450–600 m, *Hammel et al. 16193* (MO).

Anthurium santiagoense Croat, sp. nov. TYPE: Ecuador. Morona–Santiago: Proveduria, confluence of Río Bomboiza and Río Zamora, 600 m, 3°25′S, 78°27′W, *Palacios 1492* (holotype, MO 3420759; isotypes, NY, QAME). Figure 283.

Planta terrestris; internodia brevia, 1.5–2 cm diam.; cataphyllum findens in fibras lineares tenues; petiolus 24.5–27 cm longus, 1–1.2 cm diam., triangularis; lamina late elliptica ad oblongo-elliptica, 75–97 cm longa, 21.5–29 cm lata; pedunculus 20–48 cm longus, 5–11 mm diam., stipes 1–3 mm longus; spadix atropurpureus, cylindricus, 6.5–7 cm longus, 5–6 mm diam.

Description based on dried material only. Terrestrial; stem 1.5–2 cm diam.; roots few, pale grayish, pubescent, elongate, to 4 mm diam.; cataphylls probably coriaceous, 10–13.5 cm long, acute at apex, yellow-green, persisting as fine, pale, linear fibers; petioles 24.5–27 cm long, 1–1.2 mm diam., triangular, flattened to broadly sulcate adaxially, the margins acute, acutely angled abaxially; blades subcoriaceous, ± broadly elliptic to oblong-elliptic, abruptly acuminate to long-acuminate at apex (the acumen 15–20 mm long), narrowly acute at base, 75–97 cm long, 21.5–29 cm wide, broadest just above the middle, matte to weakly glossy, greenish; midrib prominently raised above, higher than broad and paler than surface below; primary lateral veins 25–33 per side, departing midrib at 60–75° angle, straight-ascending to the collective vein, slightly raised above and below, slightly paler than surface below; interprimary veins almost as conspicuous as primary lateral veins, drying raised above and below; tertiary veins visible when dried, raised; collective vein arising from near the base, drying raised above and below, equally as prominent as primary lateral veins, 7–20 mm from margin. *Inflorescences* with peduncle 20–48 cm long, 5–11 mm diam., drying greenish; spathe reflexed, subcoriaceous, green, broadly lanceolate, 7–8 cm long, 1.8–2.6 cm wide, broadest near the base, abruptly acuminate at apex, 4 mm long; stipe 7–17 mm long in front, 1–3 mm long in back; spadix deep purple, cylindroid, erect, sometimes slightly curved, 6.5–7 cm long, 5–6 mm diam. midway; flowers ± square, 1.5–2.1 mm in both directions; 7–10 flowers visible in principal spiral, 6–7 in alternate spiral; lateral tepals 0.9–1.2 mm wide, the inner margins ± straight, the outer margins 2-sided; pistils somewhat exserted; stigma ellipsoid, 0.3 mm long, droplets drying as abundant crystals and persisting; stamens emerging well above tepals; filaments translucent, flattened, 0.7 mm wide; anthers yellow, 0.4–0.5 mm long, 0.6 mm wide; thecae oblong, 0.2–0.3 mm wide, slightly divaricate; pollen fading to tan. *Infructescence* not seen.

A member of series *Multinervia*, *Anthurium santiagoense* is endemic to Ecuador, where it is known from the Río Santiago watershed (hence the name) in the Serranía de Cutucú and in Morona–Santiago Province at 600 to 1,830 m, in premontane moist and tropical moist forest life zones.

This species is characterized by its large, unusually broadly elliptic leaf blades which dry green and have numerous primary lateral veins, its relatively long, more or less triangular petioles, and its deep purple, cylindroid spadix. Characteristic also are the exserted stamens and yellow anthers.

Anthurium santiagoense is readily recognizable and not likely to be confused with any other species. The only other member of series *Multinervia* on

the eastern slope of the Andes which approaches *A. santiagoense* in size is *A. fasciale*, which has more or less oblong leaf blades with more irregular primary lateral veins, and petioles that are rounded abaxially. *Anthurium narinoense*, from the Pacific slope in Colombia, is remarkably similar in overall appearance and differs mainly by its more slender spadix.

ECUADOR. MORONA–SANTIAGO: Río Bomboiza and Río Zamora confluence, Proveduria, 600 m, 3°25′S, 78°27′W, *Palacios 1492* (MO, NY, QAME); Cordillera de Cutucú, W slopes, Logroño–Yaupi, 2°46′S, 78°6′W, *Madison et al. 3382* (SEL).

Anthurium sarukhanianum Croat & Haager, sp. nov. TYPE: Mexico. Guerrero: 2–3 km N of Zíhuatanejo, dry slopes, less than 100 m, *Haager s.n.* (holotype, MO 3582582; isotypes, MEXU, PR). [Cultivated in Praha and Brno.] Figures 277, 284.

Planta epilithica; internodia brevia, ad 3 cm diam.; petiolus U-formatus, adaxialiter sulcatus, abaxiliter rotundatus, 6–10 cm longus, 12–17 mm diam.; lamina oblanceolata ad anguste obovata, 40–75 cm longa, 17–23 cm lata; nervis primariis lateralibus 9–12 utroque; pedunculus 20 cm longus; spatha erecta, viridis multum suffusa purpurea introsum, 3.5–5 cm longa, 2.5–3.5 cm lata; spadix clavatus, 4–5 cm longus, 1.3–1.7 mm diam.

Epiphytic, to less than 1 m tall; stem short, 3 cm diam.; roots dense, 3–5 mm diam., whitish (green when moistened); cataphylls triangular, 7 cm long, weathering into brown fibers. *Leaves* erect-spreading; petioles 8–12 cm long, 12–18 mm diam., obtusely U-shaped, deeply sulcate adaxially, the margins erect to incurved (in plants cultivated under epiphytic conditions), rounded abaxially; geniculum shaped like and paler than petiole, 1.2–1.7 cm long; blades moderately coriaceous, oblanceolate to narrowly obovate, shortly acuminate at apex, acute to narrowly rounded at base, 40–75 cm long, (12)17–23 cm wide, the margins broadly and conspicuously undulate; upper surface weakly quilted, glossy, medium green, lower surface matte, slightly paler; midrib above convexly raised (with obscure medial rib on drying), becoming convexly raised toward the middle, below prominently convexly raised and weakly speckled; primary lateral veins 9–12 per side, departing midrib at 40–45° angle, moderately straight to the margin, then ascending, convex on both surfaces; interprimary veins lacking or few; major tertiary veins weakly sunken above, weakly raised and slightly darker than surface below; reticulate veins visible only on lower surface; collective vein absent. *Inflorescences* erect, much shorter than leaves; peduncle 20 cm long, 5 mm diam., drying 3.5 mm diam., 2–3× as long as petiole, terete; spathe erect, broadly ovate, 3.5–5 cm long, 2.5–3.5 cm wide, green, heavily tinged or mottled with purple on both surfaces, especially on the inner surface and along margins outside, inserted at 30° angle on peduncle, rounded and retuse at apex (the acumen short apiculate), rounded to subtruncate at base, the margins tightly recurled, meeting at 180° angle, then decurrent for a short distance; spadix medium green, clavate, sessile, held at 160° angle from peduncle, 5 cm long, 7 mm diam. near base, 1.3–1.7 mm diam. near apex, broadest just below the apex, broadly rounded at apex, evenly tapered to the base; flowers rhombic to sub-4-lobed, 2.3–2.7 mm long (fresh), 1.8–2.2 mm long (dry), 1.8–2.3 mm wide (fresh), 2–2.5 mm wide (dry), the sides almost straight to smoothly sigmoid parallel to spiral, jaggedly sigmoid perpendicular to spiral; 13–16 flowers visible in principal spiral, to 20 or more in alternate spiral; tepals semiglossy, minutely papillate, with few subrounded inclusions visible through the epidermis, drying matte, light reddish brown, weakly warty, with a thin, loose layer of wax; lateral tepals 1.2–1.5 wide, shield-shaped, the inner margins almost straight, the outer margins weakly acuminate; pistils green, umbonate, protruding weakly into the space between the tepals, the exposed area 0.5 mm diam., soon completely obscured by the stamens; stigma linear, drying 0.35 mm long; stamens emerging slowly beginning at the middle of the spadix and proceeding toward both ends, the laterals preceding the alternates, clustered tightly over the pistil; anthers whitish, 0.5 mm long, 0.6 mm wide, held at the level of the tepals; thecae narrowly ovoid, somewhat divaricate. *Infructescence* not known.

Anthurium sarukhanianum is narrowly endemic to western Mexico, known only from the type locality in the state of Guerrero, where it is locally common.

It can be confused with *A. schlechtendalii* subsp. *jimenezii* or *A. halmoorei*, which occur in similar habitats in western Mexico, but can be distinguished from either by its conspicuously clavate spadix, a feature unique among Central American species of *Pachyneurium*.

This species was first collected in 1977 by Jiri Haager of Prague, Czechoslovakia, and is named in honor of José Sarukhán, Director of the Instituto de Biología of the Universidad Autónoma de México, who assisted in the preparation of Haager's expedition in Mexico.

MEXICO. GUERRERO: 2–3 km N of Zíhuatanejo, near sea level, *Haager s.n.* (MO, MEXU, PR).

Anthurium schlechtendalii Kunth, Enum. Pl. 3: 75. 1841.

a. Anthurium schlechtendalii subsp. **schlechtendalii**. TYPE: Mexico: Hacienda de La Laguna, *Schiede & Deppe s.n.* (not seen). Figures 278, 285, 286.

Anthurium mexicanum Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1: 21. 1849. TYPE: Mexico. Veracruz: between Colipa & Misantla (not seen).

Anthurium kunthianum Liebm., Ann. Sci. Nat. Bot. ser. 4, 2: 372. 1854. TYPE: Mexico (no type cited).

Anthurium brachygonatum Schott, Prodr. Aroid. 468. 1860. TYPE: Mexico. Veracruz: Córdoba, *Kerber s.n.* (holotype, B).

Anthurium tetragonum Hook. ex Schott, Prodr. Aroid. 475. 1860. TYPE: locality unknown, Schott Aroid Drawing #541 (Schott Aroideae 541 serves as type).

Anthurium fortinense Engl., Bot. Jahrb. Syst. 25: 366. 1898. TYPE: Mexico. Veracruz: Fortín, *Kerber 9b* (holotype, B).

Anthurium tikalense Lundell, Wrightia 3:161, fig. 55. 1966. TYPE: Guatemala. Petén: Tikal National Park, on temple in Group "H," Mar. 1961, *Lundell 18198* (holotype, LL).

Epiphytic or epilithic; stem usually short, but reported to 40 cm long, 2.5–5.5 cm diam.; leaf scars obscured by root mass, to 4.2 cm wide; roots numerous, dense, ascending to descending, greenish to tan, smooth, short to moderately elongate, tapered, 3–8 mm diam.; cataphylls moderately coriaceous, curved, 7.5–16 cm long, caudate-apiculate at apex, drying brown, initially persisting intact, but eventually as a reticulum of fibers. *Leaves* erect; petioles (2.5)10–23 cm long, 4–20 mm diam., quadrangular to trapezoidal, rarely D-shaped or terete, mostly widest adaxially, flattened to shallowly sulcate and with sharp margins adaxially, sharply to bluntly ribbed abaxially, rarely rounded; geniculum somewhat thicker and paler than petiole, 1–2 cm long; blades coriaceous, obovate-elliptic to broadly oblanceolate, acute to short-acuminate at apex (the acumen apiculate), acute to obtuse at base, (16.5)30–140(175) cm long, (4.5)10–60 cm wide, broadest near or above middle, the margins prominently undulate; both surfaces matte to semiglossy, medium green above, paler below, drying greenish; midrib flat to weakly raised at base, becoming more acute (sometimes weakly ribbed), diminishing and sunken at apex above, raised and square at base below, convexly raised at apex; primary lateral veins 15–16 per side, departing midrib at 50° angle, straight almost to the margin, then arcuate toward the apex, sharply to convexly raised and paler than surface above and below; tertiary veins flat, scarcely visible above, darker than surface below; collective vein arising from near the apex, sunken above, raised below, 2–5 mm from margin. *Inflorescences* erect to spreading, sometimes pendent, shorter than leaves; peduncle 10–43 cm long, (4)6–13 mm diam., 1.6–7.4× as long as petiole, plain green or tinged with violet-purple, terete to weakly flattened and ribbed; spathe spreading to strongly reflexed, coriaceous, plain green or heavily tinged with violet-purple to red or entirely purple, narrowly triangular to lanceolate, (8)10–28 cm long, (0.7)1.5–5 cm wide, inserted at 70° angle on peduncle, acuminate at apex (the acumen inrolled), obtuse at base; spadix green to gray to brown to red to purplish violet, tapered, curved, (5.5)8–29 cm long, (7)17–20 mm diam. near base, 4–6 mm diam. near apex; flowers square, (2)2.2–2.6 mm in both directions, the sides straight to weakly sigmoid; 7–17 flowers visible in principal spiral, 10–14 in alternate spiral; tepals matte, purplish punctate; lateral tepals 1–1.3 mm wide, the inner margins convex and turned up against pistil; pistils emergent to 1 mm, dark purple to brown; stigma linear, 0.8 mm long, droplets appearing ca. 4 days before stamens emerge; stamens emerging rapidly from the base, lateral stamens emerging to midway before alternates emerge; filaments translucent, soon retracting, 0.2–0.5 mm long, 1 mm wide; anthers yellow to pale orange, 0.9 mm long in both directions, inclined over the pistil; thecae ± oblong, scarcely divaricate; pollen orange fading to cream, yeasty-scented at anthesis. *Infructescence* arching-pendent; spathe persisting; peduncle to 4 cm diam.; spadix 15.5–65(80) cm long, 4–6(9) cm diam.; berries bright red, obovoid to oblong to ellipsoid, rounded to acute at apex, 10–29 mm long, (5)6–7 mm diam.; pericarp thickened; mesocarp pulpy, white, with numerous raphide cells; seeds 2 per berry, greenish white, ovoid to oblong, flattened, 3–6 mm long, 1.5–3 mm diam., 1–1.5 mm thick, astringent to taste.

Anthurium schlechtendalii consists of two subspecies. Subspecies *schlechtendalii* ranges from Mexico (central Veracruz) to Nicaragua on the Atlantic slope, from near sea level to 1,600 m (most common below 1,000 m) in various life zones.

Anthurium schlechtendalii is characterized by its trapezoidal to quadrangular petioles, coriaceous spathe, tapered spadix, and bright red berries.

This taxon is most easily confused with *A. schlechtendalii* subsp. *jimenezii*, from the Pacific slope of Mexico, which differs by occurring in sea-

sonally drier habitats, and in its generally smaller leaves and frequently narrowly ovate, usually erect spathe. *Anthurium schlechtendalii* subsp. *schlechtendalii* may be confused with *A. upalense* in Nicaragua, where they both occur. See the discussion under that species for differences.

Anthurium schlechtendalii merges into the range of *A. salviniae* only in a few areas in the mountains of southeastern Chiapas, such as on Monte Ovando. Specimens collected in the municipios of Siltepec, Escuintla, and Acacoyagua tend to have leaf blades approaching the texture of those of *A. salviniae*, but the inflorescences and cataphylls are those of typical *A. schlechtendalii*. See the discussion following *A. salviniae* for separation characters for these two taxa.

In discussing Mexican aroids, Bunting (1965) included an illustration of a plant cultivated at Cornell University and reputedly collected by H. Moore in Mexico. This is almost certainly *A. crenatum* (L.) Kunth and perhaps represents a mixing of labels in the greenhouse. Two vouchers presumably prepared from this plant (*Bunting 1579* and *Nicolson 603*) tend to confirm this notion. *Anthurium crenatum*, as far as is known, is restricted to Puerto Rico and the Virgin Islands.

Studies of populations of *A. schlechtendalii* in Mexico and elsewhere show most morphological characters to be variable. The petioles, although usually trapezoidal in cross section with the angles moderately acute, may be broadly rounded abaxially, such as those illustrated by Schott for *A. brachygonatum* (see Schott drawing No. 473 (W)). Although Bunting (1965) considered the latter distinct from *A. schlechtendalii*, it is here believed to be one form of this unusually variable species.

BELIZE. NO FURTHER LOCALITY: *Schipp S402* (MICH, MO, NY, UC); Camp Cuello, *Lincoln 36* (MO). BELIZE: *Bartlett 11325* (MICH); Gracie Rock, 1.1–4 mi. S of mi. 22 on Western Hwy., 100 m, *Croat 23851, 23896* (MO), *Liesner & Dwyer 1472* (MO); Northern River, *Gentle 1291* (F, K); Western Highway, Gracie Rock, *Whitefoord 3171* (BM). CAYO: *Chanek 53* (MICH, MO); W of Hummingbird Hwy. at point 7 mi. S of jct. with Western Hwy., Line Transect 1, 90 m, *Spellman & Newey 1984* (MO); Waterhole camp, Vaca, *Gentle 2567* (MICH); ca. 10 km SW of San Ignacio, lx Chel Farm, along Panti Trail, 17°6′N, 89°0′W, *Balick et al. 1794* (MO); Mt. Pine Ridge, Blancaneaux Lodge, *Dwyer 12658* (MO); Río de La Flor, 6 mi. S of Grano de Oro, La Flor, 570–670 m, *Croat 23811* (MO). COROZAL: *Arnason & Lambert 17186* (MO), *Gentle 597* (MICH); Tiger Savana, 12 km W of Little Belize, 10 m, 18°11′N, 88°17′W, *Davidse & Brant 32604* (CM, M, MICH, MISSA, MO, PMA, RSA). ORANGE WALK: Orange Walk–San Pablo, *Sutton et al. 130* (BM, MO); 5 km N of August Pine Ridge, road to Trinidad, 100 m, *Davidse & Brant 32792* (MO, RSA). TOLEDO: Moffredye Lagoon, *Gentle 5372* (LL, TEX); Rideau Camp, 40 m, *Whitefoord 1801* (BM); Salamanca, 40 m, *Whitefoord 1968* (BM); 1.5 mi. S of Mayan village of San José, 5 mi. W of Colombian Forest Station, *Croat 24297, 24333* (MO); 6.7 mi. N of Columbia Forest Station, *Croat 24431* (MO), *Vanderveen 658* (MO); Maya Mts., *Boutin & Schlosser 5144* (MO); vic. of junction of Richardson Creek and Bladen Branch, 80–420 m, 16°32′N, 88°45′W, *Davidse & Brant 32025* (K, MO, NY, US); Río Grande, *Gentle 4723* (TEX). GUATEMALA. ALTA VERAPAZ: Tucurú–El Estor, above Papalha, 15 mi. W of Teleman, Finca Argentina, 250–650 m, *Croat 41536, 41551* (MO); La Tinta, *Smith 1530a* (US); Lago Izabal, Tucurú-El Estor, Route 7E, 150–300 m, *Croat 41525, 41529* (MO). ESCUINTLA: 5 km SW of Palín, *Harmon 2420* (UMO). HUEHUETENANGO: Ixcán–Finca San Rafael, *Steyermark 49411* (F); Río Trapichillo, Paso del Boquerón, below La Libertad, 1,200–1,300 m, *Steyermark 51171* (MO). IZABAL: 15.8 km S of Modesto Méndez, 70 m, *Harmon & Fuentes 2115* (MO, UMO); 7 mi. S of Puerto Barrios, 50 m, *Croat 41802* (MO); 1 mi. E of Santo Tomás, 4 mi. SW of Puerto Barrios, 50 m, *Croat 41839* (MO); E of El Estor, *Jones & Facey 3456* (NY, TEX); Quiriguá Viejo, *Standley 24053* (NY, US); Virginia-Lake Izabal, *Steyermark 38769* (F); Lago Izabal, *Jones & Facey 3437* (NY, TEX). PETÉN: 5 mi. S of entrance to Tikal National Park, *Croat 24753* (MO); Dolores, *Contreras 2254* (LL); El Paso, *Herman 14664, 14671* (MICH); *Lundell 1573* (MICH); La Libertad, *Lundell 2873* (MICH); Santa Teresa, *Lundell 2708* (MICH), *2889* (MICH, NY); Uaxactun, *Bartlett 12295, 12296* (MICH); Lago Macanche, Fallabon road, *Contreras 920* (LL); Tikal National Park, Tikal, *Bernhardt T6* (MO), *Contreras 1618* (LL), *Lundell 15410* (LL, TEX), *18198* (LL). SAN MARCOS: Volcán Tajumulco, *Steyermark 37078* (F). ZACAPA: 2 mi. N of Route CA 9, 41 mi. S of turnoff to Petén Morales, Finca Agua Fría, 150 m, *Croat 41879* (MO). HONDURAS. COLÓN: Trujillo, *Clewell et al. 4335* (MO). COMAYAGUA: Lago de Yajoa, *Zonigo 495* (TEFH), *590* (TEFH), *661* (TEFH), *867* (TEFH). COPÁN: E of Copán, *Croat 42508, 42521* (MO); 35 km E of Copán, *Blackmore & Chorley 3772* (BM). CORTÉS: 2–3 mi. SW of Omoa on road from Puerto Cortes to Guatemala border, 0 m, *Croat 42564* (MO); 7 mi. S of Portrerillos on Hwy. 1, 100 m, *Croat 42706* (MO); Guatemalan border, Corinto, *Nelson et al. 2904* (MO); La Pimienta, *Molina 5623* (F). GRACIAS A DIOS: Río Patuca, 175 m, *Clewell 4564* (MO). OLANCHO: Río Chiquito, 2 km above Río Grande, *Blackmore & Heath 1843* (BM, MO); Río Olancho, Gualaco–San Bonito Oriental, 7.4 mi. NE of San Estéban, 540 m, 15°20′N, 85°42′W, *Croat & Hannon 64362* (MO). SANTA BÁRBARA: road on NW side of Lago de Yojoa, 700 m, *Croat 42757* (B, MO); Punta Gorda, W side of Lago de Yojoa, 600 m, 14°50′N, 88°08′W, *Balick et al. 1734* (MO); Santa Rosa de Copán–San Pedro Sula, 51.3 mi. WSW of junction of main San Pedro Sula–Tegucigalpa Hwy., Hwy. 18, 500 m, 15°18′N, 88°25′W, *Croat & Hannon 63871* (MO). YORO: Coyoles, *Yuncker et al. 8132* (K, MO, NY, US); Las Flores, *Yuncker et al. 8174* (F, MO, NY); Las Minas, 60 m, *Ruiz 116* (NY); slope above Lake Yojoa, *Clewell 3114* (FSU). MEXICO. CAMPECHE: Francisco Escarcega-Champoton, 0–100 m, *Mayo & Madison 369* (K). CHIAPAS: Huixtla–Motozintla de Mendoza, 25 km from Huixtla, 650 m, *Croat 47225* (MO); Chiapa de Corzo–Pichucalco, Hwy. 195, 0.5 km from junction with Hwy. 190, 1,000 m, *Croat 46437* (MO); 20–30 mi. SW of El Jocote on road to Motozintla, 700–900 m, *Croat 40706* (MO); 20

mi. N of Ocozocoautla, road to Apitpac near Km 31, 700 m, *Croat 40653* (K, MO); 13 mi. N of Ocozocoautla, road to Apitpac near Km 21, 900 m, *Croat 40626* (MO); 6 mi. N of Ocozocoautla, road to Apitpac, 1,000 m, *Croat 40587* (MO); Palenque–Ocosingo, 27 mi. SW of Palenque, Hwy. 199, 210 m, *Croat 40319* (MO); Palenque–Bonampak, 89–90 mi. SW of Palenque, 350–370 m, *Croat 40215* (MO); along Hwy. 195, 8 mi. N of Pichucalco, 2 mi. S of Chiapas border, 80 m, *Croat 40074* (MO); San Cristóbal–Palenque, 97 km NE of San Cristóbal, San Cristóbal de Las Casas, 1,130 m, 17°27′N, 92°4′W, *Hammel et al. 15616* (MO); Palenque, 170 m, *Davidse et al. 20334* (MO); 2 mi. S of Chiapas border along Hwy. 195, 8 mi. N of Pichucalco, 80 m, *Croat 40086* (MO); Motozintla de Mendoza–Siltepec, 2 mi. W of Motozintla, 1,400 m, *Croat 47250* (MO); ruins of Bonampak, 670 m, *Hoover 282* (MO); Motozintla–Huixtla, 15 mi. S of Motozintla, 900 m, *Croat 40766* (MO); road to Finca Tres de Mayo, 3 mi. NE of El Triunfo, 13 mi. NE of Escuintla, 350 m, *Croat 43879* (F, GH, K, MO, PMA, VDB); Acacoyagua, *Matuda 19646* (DS); Angel Albino Corzo, *Ton 3880* (MAD, DS); Bochil, *Roe et al. 1132* (WIS), *Ton 2587* (DS); Chiapa de Corzo, *Breedlove 26872* (DS); Escuintla, *Matuda 17973, 19645* (MEXU); Huixtla–Motozintla, *Breedlove 28609* (DS); Ixtapa, *Laughlin 723* (DS, MICH, NY), *Laughlin 1599* (DS, MEXU, TEX); Jitotol, *Thorne & Lathrop 41341* (DS); Las Margaritas, *Breedlove 33199, 33446* (DS); Siltepec, *Matuda 18798* (MEXU); ruins of Yaxchilan, Ocosingo, *Breedlove 33872* (DS); Ocozocoautla de Espinosa, *Breedlove 29004, 36555* (DS), *30358* (DS, MO), *MacDougall H261* (NY); Pichucalco, *Breedlove 35048* (DS), *Gilly & Hernández 182* (MICH); Nuevo Acosta Solistahuacán, *Breedlove 26042* (DS), *Roe et al. 1239* (US); Raudales Mal Paso, *Quintero 3441* (MEXU); Tenejapa, *Breedlove 6242* (DS, F, MICH), *11731* (F, MICH, TEX), *Ton 350* (DS); Tuxtla Gutiérrez, *Guzman 13* (MEXU); 20 km S of Palenque, road to Ocosingo, 12–20 m, *Mayo 32* (K); Mpo. El Bosque, Simojovel de Allende, El Bosque, 1,219 m, *Breedlove 51732* (CAS, DS); Mpo. Mapastepec, Sierra de Soconusco, road to Tuxtla Gutiérrez from Hwy. 200, 5.5 mi. NW of turnoff to Mapastepec, 15°32′N, 92°48′W, *Croat & Hannon 63352* (B, MO, NY, US); Mpo. Ocosingo, 5 km SW of Santo Domingo, 120 km SE of Palenque on road to Bonampak, 600 m, *Davidse et al. 20429* (MO); Mpo. Ocozocoautla de Espinosa, 3 km N of Ocozocoautla, road to Mal Paso, 900 m, *Breedlove & Smith 21982* (DS, MO); Mpo. Palenque, 25 km S of Palenque, Cascada Mizola, road to Ocosingo, 300 m, *Breedlove & Davidse 55398* (CAS). OAXACA: no further locality, *Calderón 145* (GH); Parque Nacional de Laguna Temazcal, Temazcal, N end of rd. across dam, 150 m, 18°25′N, 96°25′W, *Hammel & Merello 15455* (MO); Teotitlán del Camino–Chilchotla, 1.2–3.8 mi. past turnoff to Huatla de Jiménez, 1,265 m, *Croat 48374, 48396* (MO); Teotitlan del Camino–Huatla de Jiménez, near junction of road to Chilchotla, 1,320 m, *Croat 48296* (MO); hill 5 km S of Tuxtepec, 100 m, *Conrad & Conrad 3251* (MO); 8.5 mi. NE of Valle Nacional, *Thurm et al. 231* (UMO); Tuxtepec–Oaxaca, 0.5–4.5 mi. S of Valle Nacional, 120–450 m, *Croat 39707, 39708, 39738* (MO); 8 km S of Matías Romero, 100 m, *Davidse et al. 30195* (CM, MO); Tuxtepec–Oaxaca, Hwy. 175, 6 mi. W of Valle Nacional, 660 m, *Croat 39756* (MO); Chinantla, *Ramírez 144* (MEXU); Matatengo Gorge, *Croat 32712, 32717* (MO); Santo Domingo Tehuántepec, *Williams 70, 83* (MICH); Temascal, *Sousa 936, 1037, 1801* (MEXU); Tuxtepec, *Calderón 844* (MICH), *Miranda 4274* (MEXU), *Moore & Bunting 8907* (BH), *Quintero 1820* (MEXU), *Rzedowski 25480, 25483* (US), *Sousa 1809, 1825* (MEXU), *Webster & Breckon 15400* (DAV); Esmeralda–Río Manea, 11.5–13.5 mi. S of Esmeralda, Uxpanapa, 90–110 m, 17°4′N, 94°45′W, *Croat & Hannon 63277* (MO, US); Trapiche de la Concepción, 1,000 m, *Liebman s.n.* (K); Cerro El Cacao (Sta. Cruz), Concepión del Progreso, Putla, 1,020 m, *Mendoza 1516-A* (MEXU); Cerro Concordia, *Morton & Makrinius 2731* (F, US); Dtto. Juchitán, Matías Romero–La Ventosa, 26 km S of Matías Romero, Route 185, 250 m, *Lorence & Jrigos 3093* (MO); Dtto. Juchitán, Mpo. Matías Romero, La Laguna–Sarabia, 7.2 km W of Esmeraldas, 200 m, 17°7′N, 94°49′W, *Wendt et al. 3634* (MO); Mpo. Santa María Chimalapa, Santa María, 300 m, 16°55′N, 94°40.5′W, *Hernández 1167* (CHAPA, MO); Dtto. Tuxtepec, E arm of Presa Miguel Alemán, Temascal, 200 m, *Neill 5400* (MO); Mpo. Acatlán, Cerro Buenos Aires, intersection 2 km S of Corrales on road to Capilla, 4 km NW of Lindero, 70 m, 18°28′N, 96°38′W, *Gereau et al. 2209* (MO); 8 mi. from Acatlán on ranch Campo Chico, *Butterwick 59* (LL); Mpo. Soyaltepec, 1 km S of S end of main dam of Presa Miguel Aleman, 140 m, 18°14′N, 96°23′W, *Gereau et al. 2237* (MO). QUINTANA ROO: 6 km N of Xelha, *Téllez & Cabrera 3233* (MEXU, MO). TABASCO: SE of Teapa, Km 4 on road to Tacotalpa, 325 m, *Croat 47894* (MO); 3 km E of Teapa along road to Jalapa, 40 m, *Croat 40109* (MO); Km 34 S of Villa Hermosa, 55 m, *Croat 40069* (K, MO, RSA, US); Baláncán, *Valdivia 2028, 2052* (XAL); NW of Cárdenas, *Barlow 26/10* (WIS); 9 km E of Teapa, road to Jalapa, 200 m, *Mayo & Madison 343* (K); Cerro Las Campanas, 3 km E of Teapa, 50 km S of Villahermosa, 50–100 m, *Conrad et al. 2866* (MO); Río Teapa, 2 km SE of Teapa, 20 m, *Davidse et al. 29522* (MO, RSA); Mpo. Tacotalpa, 0.4 km E of Tacotalpa, *Cowan et al. 3421* (MO). VERACRUZ: no further locality, *Orentt 2950* (MO); Fortín, *Kerber 9* (B); 3 km N of Catemaco, 400 m, 18°30′N, 95°10′W, *Solheim & Powers 851* (WIS); Cervecería Moctezuma hydraulic plant, 1,000–1,150 m, *Croat 39414* (DUKE, ENCB, HBG, MO, QCA, WIS); Catemaco, *Sousa & Sousa 14* (MEXU), *Menéndez 7599* (MEXU); Lago Catemaco, *Boege 1257* (CAS); Mun. Cuitlahuac, 250 m, *Hansen & Nee* (MO); Hidalgotitlán, 17°47′N, 94°38′W, *Dorantes 2862, 3099* (XAL), *Valdivia 23, 138, 614, 799, 870, 1038, 1045, 1115, 1315, 1343, 1622* (XAL), *171, 236* (MO, XAL), *191, 309, 476, 533* (MEXU), *222, 731, 1165, 1285, 1674* (MO), *275, 667, 907, 931, 1196* (MEXU, MO, XAL), *458, 1094* (MEXU, XAL), *Vázquez 582* (BM, MO, XAL); Hacienda Álvaro Obregón, 149 m, 17°47′N, 94°38′W, *Valdivia 291, 421* (MEXU, MO); Laguna, Hidalgotitlán, 160 m, 17°16′N, 94°33′W, *Valdivia 689* (MO); 5 km from La Estación de Biología de Los Tuxtlas, Laguna Escondida, 300 m, *Soto et al. 16* (MEXU, MO); 170–200 m, *Gentry et al. 32391* (MO), *Dillon et al. 1838* (MO), *Menéndez 157* (MEXU, MO), *Cochrane & Cochrane 8625* (MO), *Calzada 455* (MEXU, MO); Valle de Córdova, *Bourgeau 1787* (MEXU, MO, P); Córdoba–Veracruz, 1 mi. off Hwy., above San Juan de Gracia, 750 m, *Croat 39611* (MO), *Miranda 4894* (MEXU), *Bourgeau s.n.* (K); El Mirador, 1,200 m, *Croat 44000* (B, MO, NY, WIS); Mun. Coatepec, 670 m, *Castillo & Tapia* (MO); Actopán, *Ortega-Ortiz 563* (F, XAL), *Ortega 556* (MO); Atoyac, *Rosas 1126* (F, XAL); Barra Platanar, *Dorantes et al. 1287* (MEXU); road to Jalapa,

Dorantes 505 (CAS, F, MEXU); SE of Jalapa, *Barkley et al. 2596* (MEXU, TEX); Cordillera, *Galeotti 6055* (BR); Cuichapa, *Rosas 910* (XAL); Huatusco, *Ghiesbreght 70* (P), *Moore & Bunting 8867, 8868* (CU); Ixhautlan, *Lot 869* (CAS, MEXU); Laivaparu, *Purpus 1400* (MICH); Minatitlán, 2 km N of Uxpanapa, 150 m, 17°13′N, 94°13′W, *Wendt et al. 4828* (MO); 13.7 km E of La Laguna, 130 m, 17°19′N, 94°22′W, *Wendt et al. 5809* (MO), *Gilly & Hernandez 253* (MICH); Orizaba, *Mueller 1335* (K, NY), *Botteri & Lumichrast 1602* (P), *Mueller 1314, 1335* (NY); Cerro de Nogales, 1,700 m, *Matuda 38590* (CAS); Río La Palma, Laguna de Sontecomapan, Catemaco, 0 m, 18°33′N, 95°00′W, *Menéndez 111* (MEXU, MO); Barra de Sontecomapan, *Hernandez 608* (MEXU); Mun. Tapalapa, 500 m, *Gomez-Pompa 5105* (MO); vic. of Playa Escondida, 10 km N of Sontecomapan, 1–50 m, *Nee 26699* (F, MO, XAL); Río Coatzacoalcos, *Williams 8940* (MICH, US); Nautla, *Fay & Calzada 925* (XAL); Rancho Viejo, *Purpus 15711* (UC); Zacualpan, *Purplus 1130* (MY, UC); San Andrés Tuxtla, *Dressler & Jones 8* (MICH, NY, UC), *Hernandez & Vásquez 552* (MEXU), *Moore & Cetto 6232* (BH, MEXU); Santiago Tuxtla, *Sousa 2158, 2373* (MEXU); Valle de Río Pescados, Techacastla, 1 km SSE of Jalcomuloco, 480 m, 19°21′N, 96°45′W, *Iltis et al. 28970* (MO, WIS). YUCATÁN: *Darwin & Sundell 2137* (MO); ca. 2 mi. S of Kalcetac at Actum Spukil, *Butterwick 88* (LL, MO, TEX); 11 km S of Xcalacoop, *Utley & Utley 6495* (MO); Mun. Dzemul, 15 km N of Dzemul, 5 m, *Davidse & Davidse 29469* (MO); Chichen Itza–Mérida, 25 mi. W of Chichen Itza, *Thompson 437* (MO), *Steere 1124* (MICH); Izamal, *Gaumer 741* (F, MO); S of Mérida, *Schott 638* (F); N of Muna, *Luteyn 2528* (DUKE). NICARAGUA. BOACO: Cerro Mombachito, 500–900 m, 12°24′N, 85°32′W, *Stevens 16318* (MO), *Stevens & Grijalva 14768* (MO). CHONTALES: N of Cuapa, Juigalpa–La Libertad, *Stevens 4030* (MO). ESTELÍ: N of Estelí, Kukamonga, 800–840 m, 13°14′N, 86°21′W, *Moreno 19936* (MO); 15.8 km N of entrance to Estelí, km 167 on Hwy. 1, 825–840 m, 13°15′N, 86°22′W, *Stevens 5786, 9095* (MO). RÍO SAN JUAN: Río Oyate–San Miguelito, 100 m, *Grijalva & Almanza 3581* (MO). ZELAYA: Kurinwacito, 80–100 m, 13°8′N, 84°55′W, *Moreno 23782* (MO); Siuna, Calera, 300–345 m, 13°46′N, 84°46′W, *Ortiz 1773* (MO); El Recreo, S of Siuna, *Neill 4226, 4521* (MO); Cerro Kana Coperna, 30 km E of Siuna, 250 m, *Neill 4527* (MO); Cerro La Calera, 4 km N of Siuna, 350 m, *Neill 4289* (MO); Cerro Waylawas, 100–268 m, 13°39′N, 84°48–49′W, *Pipoly 4199, 4300, 4360, 4361, 4372* (MO), *Stevens 737, 7383, 7386, 8736, 8753, 8755* (MO).

b. Anthurium schlechtendalii subsp. **jimenezii** (Matuda) Croat, Ann. Missouri Bot. Gard. 70(2): 377. 1983. Figures 279, 280.

Anthurium jimenezii Matuda, Anales Inst. Biol. Univ. Nac. Mexico 32: 147. 1962. TYPE: Mexico. Mexico: Barranca de Zacualpan, 1,300 m, *Matuda 37245* (holotype, MEXU).

Usually terrestrial or epilithic; stem less than 30 cm long, ca. 3–4 cm diam.; roots numerous, dense, ascending to descending, tan to greenish, usually smooth, short and thick, tapered, 5–10 mm diam.; cataphylls subcoriaceous, broadly lanceolate, 6–7 cm long, acute to obtuse and weakly apiculate at apex, light green tinged with red, drying brown, persisting ± intact at the upper nodes, eventually deciduous. *Leaves* erect-spreading; petioles 2–17 cm long, 8–10 mm diam., subquadrangular to trapezoidal, flattened to broadly and sharply sulcate adaxially, the margins somewhat raised, 2–3-ribbed abaxially, the surface minutely pale-speckled; geniculum paler and thicker than petiole, becoming fissured transversely with age, 1–2 cm long; blades moderately coriaceous, oblanceolate to oblong-oblanceolate, acute to acuminate at apex (the acumen apiculate), acute to obtuse to narrowly rounded at base, 36–104 cm long, 6–32 cm wide, broadest well above the middle, the margins undulate; both surfaces glossy to semiglossy, dark green above, paler, sometimes bluish green below; midrib above flat at base, becoming obtusely to acutely angular and then weakly sunken toward the apex, below prominently higher than broad and sharply 2-ribbed at base, becoming prominently and convexly raised toward the apex and paler than surface: primary lateral veins 9–14 per side, departing midrib at 50–70° angle, weakly arcuate-ascending, raised at the midrib, becoming sunken toward the margin above, prominently raised and darker than surface below, much more prominent than interprimary veins; interprimary veins weakly sunken above, prominulous below; tertiary veins weakly sunken above, weakly raised and darker than surface below; collective vein arising in the lower half or in the upper third of blade or absent, flat to weakly sunken above, prominulous below, 2–4 mm from margin. *Inflorescences* erect, shorter than leaves; peduncle 10–54 cm long, equalling or 2–3.4× as long as petiole, medium green weakly tinged reddish, terete; spathe spreading, subcoriaceous to moderately coriaceous, green weakly tinged with purple (B & K yellow-green 6/5), lanceolate, 4–8.5 cm long, 1–2.5 cm wide, broadest just above the base, inserted at 30° angle on peduncle, oblique and narrowly acuminate at apex (the acumen inrolled), subcordate at base; spadix greenish tinged with purple (B & K yellow-green 6/5), weakly and bluntly tapered, curved, 3.5–14 cm long, 5–17 mm diam. near base, 2–5 mm diam. near apex; flowers rhombic to 4-lobed, 2.1–2.6 mm long, 2.7–2.9 mm wide, the sides straight to jaggedly sigmoid; 10–12 flowers visible in principal spiral, 6–8 in alternate spiral; tepals densely and minutely papillate, sparsely punctate, with numerous droplets at anthesis; lateral tepals 0.8–1.5 mm wide, the inner margins straight to very broadly convex, the outer margins 2–4-sided; pistils weakly emergent,

medium green, darker than tepals; stigma oblong ellipsoid, 0.3–0.5 mm long; stamens emerging promptly in a regular sequence from the base, the laterals preceding the alternates by 6 spirals, the 3rd stamen preceding the 4th by 3 spirals, held just above tepals in a circle around the pistil; anthers conspicuously white to pale orange (B & K yellow 9/5), 0.7–0.8 mm long, 0.8–1 mm wide, inclined over the pistil; thecae oblong-ellipsoid to ovoid, 0.5 mm wide, slightly or not divaricate; pollen bright yellow fading to white. *Infructescence* pendent; berries red, oblong-ellipsoid, rounded at apex, 11 mm long, 9 mm diam.; mesocarp with numerous dense raphide cells; seeds 2 per berry, tan, oblong-ellipsoid, flattened, 6 mm long, 4 mm diam., 2 mm thick, with pale punctiform raphide cells, with a sticky, gelatinous apical appendage.

Anthurium schlechtendalii subsp. *jimenezii* is endemic to the Pacific slope of Mexico and is restricted to Guerrero, Oaxaca, and Chiapas in seasonally very dry forest ("selva baja cauducifolia" and "bosque del pino-encino") at 250 to 1,500(2,325) m.

Subspecies *jimenezii* is recognized by its exclusively terrestrial or epilithic habit, thick, oblanceolate leaf blades with usually free-ending primary lateral veins, purplish spadix, green, lanceolate spathe, and red berries.

This subspecies is geographically isolated from the typical subspecies of *A. schlechtendalii*, which is found in Veracruz and northern Oaxaca and also on the eastern side of the Isthmus of Tehuantepec, but not in western Oaxaca. Subspecies *jimenezii* differs from the typical subspecies in being generally smaller, occurring exclusively on rocks and in habitats seasonally much drier, and in having usually thicker leaf blades. Matuda (1961) stressed that the taxon has peduncles relatively much longer than those of *A. schlechtendalii*. While it is generally true that the inflorescences of subsp. *jimenezii* are commonly as long as or longer than the leaves, they may also be much shorter.

Subspecies *jimenezii* is also similar to *Anthurium halmoorei*, which differs in having an ovate to ovate-elliptic spathe and mature berries that are pale greenish yellow. Also similar is *A. nizandense*, which is endemic to southern Guerrero and southern Oaxaca. *Anthurium nizandense* differs in having proportionately much longer petioles and elliptic to oblong-elliptic blades that are matte on the lower surface. In *A. nizandense* the blades are 1.3–2.5 times longer than the petioles, whereas in *A. schlechtendalii* subsp. *jimenezii* they are usually 6–10 times longer (rarely only as little as 3 times longer).

MEXICO. CHIAPAS: Mpo. Ángel Albino Corzo, Finca Cuxtepec, 1,380 m, *Breedlove 50763* (MO); Mpo. Cintalapa de Figueroa, Colonia Francisco I. Madero–Colonia A. López Mateos, 560 m, *Breedlove 50560* (MO). GUERRERO: Acahuizotla–Agua de Obispo, *Moore 5120* (BH, UC); above Acahuizotla, *Moore 6957* (BH); Acapulco–Chilpancingo, *Moore 5099* (BH); Atoyac–Filo de Caballo, Nueva Deli, 1,300–1,500 m, 17°24′N, 100°17′W, *Miller & Tenorio 639* (MO); Cerreceras, *Hinton et al. 10098* (US); Km 39–Km 40, 3 mi. N of El Rincón, 15 mi. N of Tierra Colorada, Hwy. 95, 1,500 m, *Croat 45694* (CAS, F, K, M, MO, MEX, US); Malinaltenango, S of Zacualpán, *Matuda 37245* (MEXU); Milpillas–Atoyac de Alvárez, 3.7 mi. W of turnoff on road to Chichihualco, 2,325 m, *Croat 45621B* (MO); Motozintla–Huixtla, ca. 11 mi. S of Motozintla de Mendoza on Hwy. 211, 4,800 ft., *Utley & Utley 6813* (MO); Tierra Colorada, *Rodríguez 51* (US), *Rzedowski 22809* (MICH, US); Tierra Colorada–Agua de Obispo, El Ocotito, *Crisman & Willis 199* (MICH); Dtto. Mina, Trincheras, *Hinton 10125* (GH, K, US). OAXACA: La Galera, along Hwy. 175, 2.1 mi. N of turnoff to Pluma Hidalgo, 1,340 m, *Croat 46142* (K, MO); Oaxaca–Pochutla, 55.1 mi. S of Miahuatlán, 12.9 mi. S of Suchixtepic, Hwy. 175, 1,540 m, *Croat 46093* (MO); Oaxaca–Puerto Escondido, km 195, Santa Rosa, *Rzedowski 19592* (MEXU); Pinotepa Nacional–Tlaxiaco, 15.3 mi. N of Putla de Guerrero, 49 mi. S of Tlaxiaco, Hwy. 125, 1,480 m, *Croat 45926* (F, MO); Mpo. Matías Romero, 2.2 km SW of Pachiñe, 7.5 km SW of Mogone, on road to San Juan Guichicovi, 200–300 m, 16°58′N, 95°04′W, *Wendt et al. 4816* (MO).

Anthurium schottianum Croat & R. A. Baker, Brenesia 16(Suppl. 1): 83. 1979. TYPE: Costa Rica. Limón: ca. 1 mi. N of Bribrí, ca. 40 mi. SW of Limón, 50–100 m, *Croat 43247* (holotype, MO 2584489; isotypes CR, F, K, M, NY, SEL, US). Figures 281, 287.

Terrestrial, to 1 or more m tall; stem usually less than 50 cm long, 2.5–5 cm diam.; leaf scars conspicuous, 2–4 cm wide; roots few, descending, green, with flaky or scaly epidermis when dried, often short and blunt, ca. 5 mm diam.; cataphylls coriaceous, hooked, faintly 1-ribbed at apex, 9–12 cm long, apiculate at apex, dark purple to maroon (B & K purple 2/7.5), drying brown tinged with reddish purple, persisting intact or semi-intact, eventually deciduous. *Leaves* erect to spreading; petioles 40–150 cm long, 5–10 mm diam., stiff and firm, bluntly D-shaped to subterete, weakly and shallowly sulcate to flattened adaxially, rounded (sometimes with few faint ridges) abaxially, the surface green, sometimes with dark purple tinge spreading from the base; geniculum thicker and paler than petiole, 2–3 cm long; blades subcoriaceous, ovate, gradually acuminate at apex (the acumen downturned, long-apiculate), cordate at base, 44–100 cm long, 33–50 cm wide, broadest below or near the middle, the margins shallowly undulate, flat to revolute; anterior lobe 32–80 cm

long, the posterior lobes 12–21 cm long, directed inward, rounded at apex; sinus usually narrowly triangular to closed, sometimes with overlapping lobes; upper surface matte to semiglossy, medium green, lower surface semiglossy, slightly paler; midrib above acutely raised at base, becoming sharply and narrowly raised toward the apex and paler than surface, below convexly raised at base, becoming sharply acute toward the apex; basal veins 5–9 pairs, not coalesced, sharply and narrowly raised above, less so below; primary lateral veins 9–20 per side, departing midrib at 35–50° angle, slightly arcuate-ascending, faintly loop-connecting, sharply raised above, less prominently and paler than surfaces below; interprimary veins few, narrowly raised above and below, paler than surface above; tertiary veins flat to weakly sunken above, somewhat raised below, paler than surface above and below; reticulate veins scarcely visible above, scarcely raised below, prominulous when dried on both surfaces; collective vein arising from 2nd basal vein, slightly sunken above, slightly raised below, obscure above when dried, slightly raised and paler than surface below, 2–6 mm from margin. *Inflorescences* erect, much shorter than leaves; peduncle sometimes absent or to 20 cm long, 4–5 mm diam., 0.2–0.4× as long as petiole, dark purple, terete; spathe spreading-reflexed to twisted, coriaceous, dark purple tinged with green (B & K red-purple 2/7.5), ovate-lanceolate, 6.5–15 cm long, 1.6–3.5 cm wide, broadest near base, inserted at 45° angle on peduncle, abruptly acuminate at apex (the acumen inrolled), rounded to subcordate at base, the margins meeting at 90–180° angle and stiffly rolled under; spadix deep red-violet to purple (B & K purple 2/7.5), cylindroid-tapered, 4–14 cm long, 7–9 mm diam. near base, 4–5 mm diam. near apex; flowers rhombic to square, 2.6–3 mm long, 1.5–3.5 mm wide, the sides ± straight; 4–6 flowers visible in principal spiral, 5–8 in alternate spiral; tepals matte, densely greenish punctate, minutely papillate; lateral tepals 1.9 mm wide, the inner margins straight to convex; pistils not emergent, rectangular, minutely and barely exposed and somewhat glossy, violet-purple (also reported as white); stigma slitlike; stamens emerging slowly from the base, in a regular progression, weakly exserted then retracting, grouped in a tight cluster above pistil; filaments flattened, translucent, 0.3–0.5 mm long, 0.6–0.7 mm wide; anthers yellow, 0.5–0.6 mm long, 0.7–0.9 mm wide, inclined over pistil; thecae ellipsoid, scarcely divaricate; pollen yellow (B & K yellow 9/5), sweet-scented; *Infructescence* with spathe usually persisting; spadix to 35 cm long, 2.5 cm diam., bearing berries in the basal portion only; berries pinkish with metallic sheen, darker in the apical third, obovoid, acute to rounded at apex, 9–10 mm long; pericarp thin; seeds 2 per berry, light brown, flattened, 6 mm long, 5 mm diam., 2 mm thick.

Anthurium schottianum is known only from a region of premontane wet forest-basal belt transition in extreme southwestern Costa Rica at less than 100 m. It will no doubt be found elsewhere in Costa Rica and Panama on the Atlantic slope.

This species is distinguished by its large, thin, ovate leaf blades with scarcely any posterior rib (i.e., all basal veins are free to the petiole), and by its short peduncle, purple spadix and ovate-lanceolate, often purplish, frequently twisted spathe. An unusual feature is the seasonal appearance of several inflorescences at the same time. The species has no known relatives.

COSTA RICA. LIMÓN: 1 mi. NE of Bribrí, 40 mi. SW of Limón, 50–100 m, *Croat 43247* (CR, F, K, M, MO, NY, RSA, SEL, US); Reserva Biológica Hitoy Cerere, Río Cerere to 1 km upstream from Quebrada Barrera, SW of Valle La Estrella, 90–200 m, 9°40.5′N, 83°2′W, *Grayum & Hammel 5764* (B, MO); Río Catarata, N of Bribrí, *Utley 5500* (DUKE); Río Sixaola, Bribrí–Caribbean coastal plain, 50–100 m, 9°37′N, 82°49′W, *Baker & Burger 69* (MO), *Burger et al. 10391* (F, MO), *10300* (MO).

Anthurium seibertii Croat & R. A. Baker, Brenesia 16(Suppl. 1): 85. 1979. TYPE: Panama. Chiriquí: wooded slopes on Cerro Horqueta, 1,650 m, *Croat 26976* (holotype, MO 2251853; isotypes, B, BM, CM, CR, F, GH, K, M, NY, PMA, RSA, US). Figures 282, 288, 291.

Epiphytic or epilithic or terrestrial; stem thick, short, 3–6 cm diam.; leaf scars mostly inconspicuous, ca. 2 cm wide; roots numerous, spreading to descending, pale green, pubescent, moderately thick and elongate, blunt, 3–6 mm diam.; cataphylls moderately coriaceous, lanceolate, prominently 1-ribbed near the apex, 12–21 cm long, acute at apex with subapical apiculum to 5 mm long, light green, drying tan (B & K yellow-red 8/5), persisting semi-intact, eventually deciduous. *Leaves* erect-spreading; petioles 10–55 cm long, 6–10 mm diam., stiff, firm, subquadrangular, flattened adaxially, the margins sometimes raised, 1–5-ribbed abaxially, the surface pale-speckled; geniculum thicker and paler than petiole, becoming fissured transversely with age, 1.5–3 cm long; blades coriaceous to subcoriaceous, oblong-elliptic, gradually acuminate at apex (the acumen apiculate), acute to obtuse to narrowly rounded at base, 45–85 cm long, 4–16 cm wide, broadest at or near the middle, the margins flat to slightly undulate;

upper surface glossy to semiglossy, medium to dark green, lower surface matte to glossy, conspicuously paler; midrib convexly raised above, paler than surface, sharply and obtusely raised below, slightly paler than surface; primary lateral veins many per side, departing midrib at 50–60° angle, arcuate-ascending, prominently loop-connecting, prominently sunken above, raised and darker than surface below; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins obscure above, weakly visible below; reticulate veins obscure above, mostly obscure below, drying partly prominulous on both surfaces; collective vein arising from near the base, equally as prominent as primary lateral veins, sunken above, raised and darker than surface below, 2–7 mm from margin. *Inflorescences* erect to spreading, shorter than leaves, 1–5 per plant; peduncle 30–60 cm long, 6–10 mm diam.; 1.5–3 × as long as petioles, green, sometimes tinged with purple, terete with single dorsal rib; spathe reflexed, often becoming recurled, subcoriaceous, plain green or tinged with purple (B & K yellow-green 7/10), oblong-lanceolate, 10–17 cm long, 2.5–4.3 cm wide, broadest near the base, inserted at 50° angle on peduncle, gradually and narrowly long-acuminate at apex, rarely short-acuminate (the acumen inrolled), rounded (scarcely decurrent) at base, the margins meeting at ca. 140° angle; stipe 13 mm long in front, 1 mm long in back; spadix violet-purple (B & K blue-purple 2/10), cylindroid-tapered, 10–20 cm long, 7–13 mm diam. near base, 5–6 mm diam. near apex; flowers 4-lobed at apex, 2–2.5 mm in both directions, the sides jaggedly sigmoid; 7–10 flowers visible in either spiral; tepals matte; lateral tepals ca. 1.5 mm wide, the inner margins straight; pistils rectangular, orange-yellow; stigma rectangular, ca. 0.7 mm long, droplets persisting for several days before stamens emerge; stamens emerging ± rapidly from the base, held just above tepals at anthesis; filaments not exposed; anthers pale orange, ca. 0.5 mm long, 1 mm wide; thecae ellipsoid, scarcely divaricate; pollen white. *Infructescence* pendent; spathe often deciduous; spadix 22–30 cm long, ca. 2 cm diam.; berries orange, obovoid, flat to rounded at apex, 10–12 mm long; mesocarp mealy, orange, sweet-tasting but pungent; seeds 2 per berry, ± oblong with rounded corners, ca. 5 mm long, 4 mm diam., 2 mm thick.

Anthurium seibertii ranges from central Costa Rica to western Panama at 1,000 to 3,000 m in premontane wet, lower montane wet, and lower montane rain forest life zones.

This species is characterized by its oblong-elliptic leaf blades, subquadrangular petioles, violet-purple spadix, and orange berries.

Anthurium seibertii is very similar to *A. protensum*. These species share similar strap-shaped leaves, purple spadices, and orange berries. *Anthurium protensum* differs in having a nearly terete petiole, while *A. seibertii* has petioles that are quadrangular in cross section and prominently ribbed abaxially. Leaves of *Anthurium protensum* are also usually pendent and generally smaller than those of *A. seibertii*.

COSTA RICA. ALAJUELA: San Carlos, 1,375 m, *Smith 1498* (NY). LIMÓN: Cerro Pittier, Valle de Silencio, 6,000–6,500 ft., *Antonio 1675* (cultivated at MO). PUNTARENAS: Cantón de Coto Brus, cultivated at Las Cruces Tropical Botanical Garden, 6 km W of San Vito de Java, 1,200 m, *Croat 57259* (MO); Cerro Burú, upper slopes, 2,000–2,300 m, 9°0′N, 82°49′W, *Davidse et al. 23789, 23790, 23791, 23831* (MO); Cordillera de Talamanca, Cerro Frantzius–Cerro Pittier, Río Canasta, 9.4 air km NW of Agua Caliente, 1,500–1,600 m, 9°2′N, 82°59′W, *Davidse et al. 28395* (MO); Cerro Frantzius to Valle de Silencio, 2,000–2,500 m, 9°3–6′N, 82°58–59′W, *Davidse et al. 28565* (CR, MO); headwaters of Río Bella Vista–Sitio Cotón on Río Cotón, 1,800-2,200 m, 9°49–57′N, 82°46–49′W, *Davidse et al. 25535* (MO); Tres Colinas, 1,800–1,850 m, 9°7′N, 83°4′W, *Davidse et al. 25602* (K, MO, RSA), *25613* (CR, K, MO), *25636* (B, MO); Tres Colinas–Cerro Bekom, 2,300 m, 9°7–10′N, 83°4′W, *Davidse & Herrera 26179, 26183* (CR, MO); Sitio Coto Brus, 1,800–1,900 m, 8°59′N, 82°46′W, *Davidse 24528, 24534* (MO); Monteverde Reserve, 11°20′N, 84°40′W, *Hepper 110* (BM); Río Burú, upper part, 2,010 m, *Gómez et al. 21800* (CR, MO); Río Cotoncito, Las Tablas, Zona Protectora, *Chacón et al. 1768* (DUKE, MO, RSA). SAN JOSÉ: Sierra–San Cristóbal Sur, 1–2 km from Sierra, 1,900 m, *Utley & Utley 3059* (MO); El General, 1,040 m, *Skutch 2626* (F, MO). PANAMA. CHIRIQUÍ: 1.5 mi. W of Cerro Punta, 1,700 m, *McDaniel 10161* (IBE); Bambito, 2,000 m, *Correa & Lazor 1407* (PMA); Bambito–Cerro Punta, *Croat 10555* (MO); Cerro Punta–Quebrada Iglesia, *Croat & Porter 16063* (M, MO, RSA, U, VEN); 3.7 km E of bridge NE of Cerro Punta, on road through Bajo Grande, 2,250–2,400 m, 8°50′N, 82°32′W, *Stevens 18226* (MO, PMA); Volcán, *Antonio 1059* (MO); 3.5 km NE of Boquete, end of road along Río Palo Alto, *Hammel 5667* (MO); Barú Summit, W end of high ridge W of summit, 3,000 m, *Hammel et al. 6916* (MO); Boquete Region, Quiel Road, 10 km above Boquete, 1,830 m, *Proctor 31816* (LL); Bajo Mono, Quebrada Chiquero, 1,500 m, *Woodson & Schery 599* (MO); Palo Alto, E of Boquete, 1,670 m, *Stern et al. 1076* (MO); Boquete, Monte Rey, *Croat 15743* (MO, NY), *15844* (MO), *Woodson & Schery 265* (MO); Boquete, La Popa, 1,500–2,500 m, *D'Arcy 10853* (MO); Boquete, *Folsom 2194* (MO); Cerro Horqueta, 1,500–1,830 m, *Croat 26976* (B, CM, CR, F, GH, K, M, MO, NY, PMA, RSA, US), *Dwyer 8749* (MO, DUKE); 1,870–2,470 m, *Averett et al. 1084* (MO); NW of Boquete, 1,670–1,930 m, *Burch 553* (MO); above Boquete, on E slope above Quebrada Horqueta, 1,660–1,700 m, 8°49′N, 82°29′W, *Cochrane et al. 6243* (MO, WIS); Cerro La Trompeta, Palo Alto, 4.5 mi. NE of Boquete, 2,070 m, *Hammel 7464* (MO); Cerro Pate Macho, 1,630–

1,780 m, 8°46′N, 82°25′W *Croat 66358* (MO); headwaters of Río Palo Alto, above Palo Alto, 1,700–2,100 m, 8°47′N, 82°22′W, *Knapp & Schmalzel 4794* (MO, USM); N fork of Río Palo Alto–Cerro Pate Macho, 6 km NE of Boquete, 1,500–1,700 m, *Grayum et al. 6361* (CM, MO, NY), *Stein et al. 1183* (MO); Cerro Punta, Raul Castro's house, Guadalupe, 2,000–2,330 m, *Folsom 6034, 6035* (MO); 0.5 mi. SE of Entre Ríos, 1 mi. by road from Cerro Punta, 2,000 m, *Croat 48568* (K, MO, PMA, SEL); 2.2 mi. below Cerro Punta, W side of Volcán Chiriquí, 200 m, *Luteyn 902* (MO); Alto los Guerra, road W of Bambito, 1,800–2,000 m, 8°53′N, 82°37′W, *Hamilton & Krager 3894* (B, K, MO); E of Bajo Choro, N slope of Barú, 2,000–2,170 m, *Hammel 2994* (MO); Quebrada Bambito, S of Cerro Punta, *Lazor 2727* (MO); Las Cumbres, W of Cerro Punta, 2,470 m, *D'Arcy et al. 13196* (MO); Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 882, 982* (MO); Bambito–Cerro Punta, Volcán de Chiriquí, *Croat 10551* (MO); Las Nubes, 2,000 m, *Croat 26427* (MO, SEL), *Croat 26494* (B, CAS, CM, DUKE, K, MO); N of Audubon cabin, *Croat 13618* (MO); along road to Cerro Punta, 8 km NW of Boquete, 5.5 km NW of Alto Quiel, 1,600 m, *Nee 9945* (MO); E of Cerro Punta, road to Paseo Respingo, 2,330 m, *Hammel et al. 6623* (MO); Río Caldera, Bajo Mono, NW of Boquete, 2,130 m, *D'Arcy et al. 12761* (MO); Río Chiriquí Viejo, upper part, Monte Lirio, 1,300–2,000 m, *Allen 1506* (MO), *Seibert 172* (MO, NY), *Seibert 289* (MO); Dtto. Boquete, Bajo Chorro, *Davidson 225, 276* (MO); Dtto. Bugaba, Cerro Pando, Santa Clara, Hartman's finca, 1,300 m, 8°50′N, 82°44′W, *van der Werff & Herrera 7126* (B, MO), *7303* (MO, RSA).

Anthurium selloum K. Koch, Ind. Sem. Hort. Berol. App. 8. 1855. TYPE: St. Johns, Virgin Islands, *Krebs s.n.* (lectotype, C). Figures 193A, 289.

Pothos macrophylla Sw., Prodr. 33: 1788; Fl. Ind. Occ. 3: 269. 1806. TYPE: Jamaica? Not seen.

Anthurium macrophyllum (Sw.) Schott (1829) non D. Don in Sweet (1839) nec Endl. ex Griseb. (1864), Prodr. Aroid. 516. 1860.

Description based on dried material only. Epilithic; stem and cataphylls unknown. *Leaves* with petioles ca. 34–45 cm long, ca. 7 mm diam., mostly spreading, apparently D-shaped, slightly flattened laterally, sulcate adaxially, with the margins acutely raised, rounded abaxially; geniculum thicker and paler than petiole, 1–1.5 cm long; sheath 4 cm long; blades subcoriaceous, oblong-ovate, somewhat triangular, acute to weakly and shortly acuminate at apex (the acumen ca. 10 mm long), broadly and shallowly cordate at base, 36–46 cm long, 14–19 cm wide, broadest in the basal third, the margins conspicuously and broadly undulate; apex of posterior lobes rounded; sinus parabolic-arcuate, 3 cm deep; both surfaces weakly glossy, yellowish brown and greenish in part; midrib apparently convexly raised above and below; major veins convexly raised, paler than surface and yellowish above and below; basal veins 3–4 pairs, 2nd & 3rd to 4th coalesced for up to 1.3 cm; primary lateral veins 3–5 per side, departing midrib at 25–45° angle, mostly straight, sometimes arcuate to the margin; interprimary veins sometimes present, ranging from not as conspicuous as to almost as conspicuous as primary lateral veins; tertiary veins conspicuous above and below; reticulate veins obscure above, weakly visible below; collective vein arising from uppermost ½ or ⅓ of the blade, less prominent than primary lateral veins, to 11 mm from margin. *Inflorescences* apparently ± spreading; peduncle 39–73 cm long, 2–4 mm diam., 1.1–2.1 × as long as petiole, pale green, subterete; spathe semi-erect to reflexed, thinly coriaceous, pale green, oblong-lanceolate, 7.5–13.5 cm long, 0.8–1.4 cm wide, broadest near the base, inserted at 40–50° angle on peduncle, narrowly acuminate to caudate at apex (the acumen 10–20 mm long), acute to obtuse at base; spadix dark maroon purple to brownish purple, long-tapered, sessile, held at 150–170° angle from peduncle, 14–27 cm long, 6–8 mm diam. near base, 2–3 mm diam. near apex, broadest near the base; flowers rhombic, 1.6–2.4 mm long, 1.7–2.8 mm wide, the sides jaggedly to smoothly sigmoid; 7–8 flowers visible in principal spiral, 4–6 in alternate spiral; tepals roughened, lateral tepals 1.1–1.5 mm wide, the inner margins usually broadly convex, sometimes straight, the outer margins 2-sided; stigma broadly ellipsoid, 0.4–0.6 mm long, densely brush-like; filaments apparently flattened, 0.4–0.5 mm long, 0.5–0.7 mm wide; anthers yellow, 0.5–0.6 mm long, 0.4–0.5 mm wide; thecae oblong, not divaricate. *Infructescence* not seen.

Anthurium selloum is endemic to the West Indies, known only by a few collections from elevations of 300 m or less, on two of the U.S. and British Virgin Islands (St. John and Tortola, respectively).

This species is distinguished by its somewhat triangular, shallowly cordate leaf blades broadest in the lower third and with 3–4 pairs of basal veins, and by the long-tapered, dark maroon-purple spadix. It is unlikely to be confused with any other species in the West Indies, or anywhere else.

Engler (1905) questionably placed *Pothos macrophylla* Sw. in synonymy with *A. selloum*, perhaps based on Schott's (1860) placement of *A. selloum* in synonymy with *A. macrophyllum* Schott.

BRITISH VIRGIN ISLANDS. TORTOLA: High Bush, 75 m, *Britton & Shafer 714* (NY, US). U.S. VIRGIN ISLANDS. ST JOHN: *Raunkiaer 2669* (C); Bordeaux, 300 m, *Britton*

& Shafer 560 (NY, US), *Krebs s.n.* (C). WEST INDIES. WITHOUT LOCALITY: *Martens s.n.* (BR), *Brown s.n.* (K).

Anthurium simpsonii Croat, sp. nov. TYPE: Peru. Tumbes: Dtto. Matapalo, road to Campo Verde, *Simpson & Schunke 392* (holotype, F 1771582). Figure 290.

Planta epiphytica; internodia ca. 1.5 cm diam.; cataphyllum persistens velis fibrarum reticularum; petiolus 6 cm longus, ca. 6 mm diam., D-formatus; lamina oblongo-oblanceolata, 66 cm longa, 8.5 cm lata; pedunculus 23–25 cm longus; spatha oblanceolata, ca. 5 cm longa, ca. 8 mm lata; spadix purpureus, cylindricus, ca. 5 mm diam.

Description based on dried material only. Epiphytic; stem ca. 1.5 cm diam.; roots numerous, dense, gray-brown and shortly woolly-pubescent, moderately thick and elongate, somewhat tapered at apex, 3–5 mm diam.; cataphylls subcoriaceous, 11.5–12 cm long, acuminate at apex, tan, persisting intact, eventually as a reticulum of fibers. *Leaves* erect or somewhat spreading; petioles 6 cm long, ca. 6 mm diam., D-shaped, probably flattened adaxially, rounded or multi-ribbed abaxially; geniculum slightly darker than petiole, ca. 1 cm long; blades subcoriaceous, oblong-oblanceolate, acute at apex (the acumen apiculate), acute at base, 66 cm long, 8.5 cm wide, broadest at or above the middle; upper surface glossy, lower surface semiglossy; both surfaces matte, grayish green; midrib flat to convexly raised above, concolorous with the surface, prominently and convexly raised below, paler than surface; primary lateral veins ca. 22 per side, departing midrib at 50–60° angle, ± straight to the collective vein, raised above and below, slightly paler than surface below; interprimary veins prominulous below; reticulate veins visible below; collective vein arising from near the base, raised above and below, less prominent than primary lateral veins, 1–3 mm from margin. *Inflorescences* with peduncle 23–25 cm long, ca. 3 mm diam., ca. 5× as long as petioles, terete; spathe, yellowish brown, oblanceolate, ca. 5 cm long, 0.8 cm wide, acute at base, the margins meeting at an acute angle; stipe 7 mm long in front, 3 mm long in back; spadix purplish, cylindroid, erect, ca. 5 mm diam.; flowers ± square; 5–7 flowers visible in principal spiral, 7–9 in alternate spiral; tepals deep purple with light tips; lateral tepals 0.9–1.2 mm wide, the inner margins straight, the outer margins 2-sided; pistils glossy, wine-red; stigma probably slitlike; anthers 0.4 mm long, 0.4–0.5 mm wide; thecae oblong, 0.2 mm wide, slightly or not at all divaricate. *Infructescence* with spathe persistent; spadix 12.5 cm long, 1.8 cm diam.; berries purple, ovoid, acute at apex, 6.5 mm long, 5.5 mm diam.; mesocarp translucent, gelatinous, orange; seeds 2 per berry, yellow-brown, flattened, 3.5–3.7 mm long, 2.7 mm diam., 0.9–1 mm thick, enveloped by gelatinous, translucent substance.

Anthurium simpsonii is known only from the type collection from the Department of Tumbes in northern coastal Peru, at 600 to 800 m in the subtropical dry forest life zone.

This species is characterized by its small size, very short petioles, and oblong-oblanceolate blades with collective veins arising from near the base, as well as by the long, rather slender spadix, deep purple flowers, and wine-red fruits. It is not likely to be confused with any other species. The only other species of sect. *Pachyneurium* that occurs in this part of Peru is *Anthurium barclayanum*, a much larger plant with leaves drying dark brown (not grayish) and collective veins arising from near the apex.

The new species is named in honor of Donald Simpson, formerly of the Field Museum of Natural History (F), who collected the type when he headed the Flora of Peru Project.

PERU. TUMBES: Prov. Zarumilla, Dtto. Matapalo, Bosque National de Tumbes, Campo Verde, 600–800 m, *Simpson & Schunke 392* (F).

Anthurium solitarium (Vell. Conc.) Schott, Prodr. Aroid. 478. 1860. Figures 292, 293, 295.

Pothos solitarius Vell. Conc., Fl. Flum. 9: t. 123. 1825 [1829]. TYPE: Brazil. Rio de Janeiro. (The plate cited above serves as the type.)

Anthurium glaziovii Hook. f., Bot. Mag. t. 6833. 1885. TYPE: Brazil. Rio de Janeiro, *Glaziou 17333* (holotype, B, photo seen; isotype, K).

Anthurium nobile Engl., Bot. Jahrb. Syst. 25: 366. 1898. TYPE: Brazil. Rio de Janeiro, *Glaziou 9039* (holotype, B; MO, photo).

Epiphytic or epilithic; stem 1.5–4 cm diam.; roots descending, velutinous, appearing inflated or with air spaces inside when dried, sharply tapered at apex, 2–9 cm long, 3–10 mm diam.; cataphylls lanceolate, 6–11 cm long, acuminate at apex with subapical apiculum to 5 mm long, drying brown, persisting semi-intact at apex and eventually weathering into coarse, linear fibers. *Leaves* erect-spreading; petioles (2)6–28(32) cm long, 5–9 mm diam., spreading, C-shaped to thicker than broad, narrowly and deeply sulcate with obtuse to acute margins adaxially, rounded abaxially, the surface dark green, pale-speckled; geniculum slightly thicker and paler than petiole, 1–1.5 cm long; sheath 2.5–4 cm long; blades subcoriaceous to

coriaceous, obovate to oblanceolate, often somewhat elliptic, short-acuminate to acute and apiculate at apex, obtuse to semi-rounded or weakly subcordate at base, 26–70(80) cm long, (6)10–23(27) cm wide, broadest at or near the middle, the margins weakly and broadly undulate; upper surface semiglossy, medium green, lower surface weakly glossy, paler below; both surfaces drying matte to semiglossy, yellowish brown; midrib flat to obtusely raised or obtusely sulcate at base, becoming convexly raised, sometimes sharply acute toward the apex above, obtusely to acutely raised, sometimes faintly 1–3-ribbed at base below; primary lateral veins 5–12 per side, departing midrib at (25)40–60(70)° angle, ± straight, becoming arcuate near margin, raised in grooves or weakly to prominently raised on upper surface, prominently raised and stout below, paler than surface; interprimary veins weakly raised above and below when visible, darker below; tertiary veins prominulous, weakly raised to weakly sunken above, moderately visible or obscure above, very weakly raised below; collective vein arising from near the apex or absent, if present sunken above, raised below, 10–20 mm from margin. *Inflorescences* erect or erect-spreading, or somewhat pendent; peduncle (15)30–102 cm long, 3–5 mm diam., 1.3–16× as long as petiole, green sometimes tinged with purple, terete, pale- to dark-speckled; spathe spreading, coriaceous, green tinged with purple adaxially, oblong to lanceolate, 6–25 cm long, 1.5–2 cm wide, broadest near the base, acuminate at apex (the acumen inrolled, 5–10 mm long), obtuse to acute at base, often decurrent; spadix dark maroon or purple, mostly subsessile (rarely stipitate to 30 mm), tapered, curved, 12–33 cm long, 4–14 mm diam. at base, 3–7 mm diam. at apex, broadest at the base; flowers rhombic, 1.8–3.6 mm long, 1.2–2.6 mm wide, the sides ± straight to sigmoid; 6–10 flowers visible in principal spiral, (6)10–12 in alternate spiral; tepals matte; lateral tepals 1–1.6 mm wide, the inner margins broadly convex, the outer margins 2-sided; pistils not emergent; stigma linear becoming ellipsoid, possibly becoming circular, sometimes appearing somewhat caviform when dried, 0.4–0.7 mm long; stamens emerging in a regular sequence; the laterals preceding the alternates by 13–20 spirals, held at edge of the tepals, inclined over and obscuring the pistil; filaments not exserted; anthers 0.4–0.5 mm long, 0.8–0.9 mm wide; thecae ovoid, 0.3–0.4 mm wide, slightly divaricate; pollen golden. *Infructescence* with spathe persisting; spadix 19–40 cm long, 11–18 mm diam.; berries purple-red, more or less oblong, the basal tepalar fibers strongly adherent, 5–6 mm long, 2–3 mm diam.; pericarp with raphide cells; mesocarp ± dry; seeds 1–2 per berry, covered with raphides, ellipsoid, 4–4.4 mm long, 1.8–2 mm diam., 0.8–1 mm thick, with a gelatinous appendage.

Anthurium solitarium is known from the states of Espírito Santo, Goiás, Minas Gerais, and Rio de Janeiro in Brazil from 300 to 1,300 m, where it is epiphytic or epilithic in mainly primary forest habitats.

This species is recognized by its thickly coriaceous, obovate or oblanceolate blades, with the primary lateral veins running straight from the midrib to the margin, and then steeply and arcuately rising along the margin. Also distinctive is the maroon to purple spadix and prominently decurrent spathe.

Anthurium solitarium is not easily confused with any other Brazilian species or with species from other areas.

Several collections are noteworthy. *Glaziou 9039*, the type of *Anthurium nobile* (here synonymized), is unusual in having a prominently stipitate (nearly 3.5 cm) spadix, instead of the more common sessile to weakly stipitate condition. *Croat 53794*, a sterile collection from cultivation, may possibly represent a distinct species. It differs in having a thicker blade with less conspicuous tertiary veins, as well as having the primary lateral veins and the midrib drying pale and wrinkled. *Croat 53699*, also of cultivated origin, is unusual in having a collective vein arising from one of the primary lateral veins almost at the middle of the blade. Generally, the collective vein of *A. solitarium* is lacking or strictly apical.

BRAZIL. BAHIA: Santa Cruz de Cabrália (cultivated at Sitio Burle-Marx), 16°18′S, 39°01′W, *Harley et al. 20316* (K). ESPÍRITO SANTO: Domingos Martins, property of Roberto Kautsky, *Croat 57165* (cultivated) (MO), *61808* (MO, R), *61817* (MO, R); Domingos Martins–Santa Maria Jetibá, 31 km N of Domingos Martin, ca. 0°20′S, 40°40′W, *Croat 61893* (MO, R); 0.8 km N of town, 525 m, 20°22′S, 40°40′W, *Croat 61798* (MO, R); Colatina–Vitoria, 45 km E of Colatina, *Belem 3833* (NY), *Croat 61894* (MO, R); Domingos Martins–Santa Maria, 845 m, *Plummer 194* (cultivated at Kew, #275-79-02469) (K). GOIÁS: 12 km S of Caiaponia, *Hutchison 8505* (MO). MINAS GERAIS: Paraibuna, *Heringer 7660* (RB, UB); 17 km E of Cambuquira, Hwy. 267 to Caxambu, 950 m, *Davidse & Ramamoorthy 10670* (MO); north of Caxambu, *Clayton 9/22/1951* (NY). RIO DE JANEIRO: *Glaziou 9039* (B), *17333* (K); cultivated by Burle-Marx, San Carlos, *Croat 53699* (MO, NY, RB), *53708*, *53711*, *53712*, *53713* (MO, RB); Cultivated by Luis Gurken, San Carlos, *Croat 53794*, *53792* (MO); Friborgo, 1,000 m *Croat 53793* (MO); Serra da Carioca, Rio de Janeiro, Macico da Tijuca, 300 m, *Croat 53670* (MO); Serra dos Orgãos, *Luetzelburg 6061* (RB); E of Rio Maio, Teresopolis, *Vidal 953*

(RB); Neves Armond, Carmo, *RB 43978* (RB); Mpo. Petropolis, Rodovia Washington Luis, 420 m, *Martinelli 3080* (RB); Reserva do IBDF, Mata do Facão, estrada Fazenda Inglesa para Pati do Alferes, 1,100–1,200 m, *Cavalcante & Marinelli 541* (K); Mpo. de Santo Antônio de Pádua, BR 393, *Pirani et al. 268* (K, MO, SPF); Mpo. Teresopolis, Parque Nacional da Serra dos Orgãos, 1,300 m, *Vidal 5557* (R).

Anthurium solomonii Croat, sp. nov. TYPE: Bolivia. La Paz: Prov. Yungas: 32.1 km N of Yolosa on road to Caranavi, *Solomon & Escobar 12494* (holotype, MO 32475329-30; isotype, LPB). Figures 296, 345, 346.

Planta epilithica aut terrestris; internodia brevia, ad 5 cm diam.; cataphyllum ad 19 cm longum, persistens semiintactum demum fibris linearis findens; petiolus 7–21 cm longus, 8–10 mm diam., D-formatus, 1-costatus adaxile, 1–2-costatus abaxile; lamina oblanceolata ad oblongo-oblanceolata, (39)65–94 cm longa, (9)18–35 cm lata; pedunculus (4)10–26 cm longus, ca. 5 mm diam.; spatha lanceolata, utra 6 cm longa, ca. 1.7 cm lata; spadix longeus contractus vel cylindricus, 7.5–19.5 cm longus, 9 mm diam.; baccae laete roseo-purpureae.

Description based on dried material only. Epilithic or terrestrial; stem to 5 cm diam.; roots numerous, gray, finely pubescent, short, 2–4 mm diam.; cataphylls probably subcoriaceous, to more than 19 cm long, brown-gray, persisting semi-intact, eventually as fine linear fibers. *Leaves* with petioles 7–21 cm long, 8–10 mm diam., D-shaped, with an obtuse medial rib and acute, somewhat raised margins adaxially, 1–3-ribbed abaxially; geniculum drying darker than petiole, 0.7–1 cm long; sheath 6 cm long; blades subcoriaceous, oblanceolate to oblong-oblanceolate, acute at apex (the acumen apiculate), narrowly rounded at base, (39)65–94 cm long, (9)18–35 cm wide, broadest above the middle, the margins undulate; both surfaces glossy, matte to glossy, brown to greenish; midrib sharply and prominently acute above, below higher than broad and obscurely 3-ribbed at base, becoming convexly raised toward the apex; primary lateral veins (10)15–19 per side, departing midrib at 40–90° angle, straight, sometimes broadly arcuate, convexly raised on both surfaces; interprimary veins few; tertiary veins raised above and below; reticulate veins raised below; collective vein arising from lower third of the blade or absent in young plants, less prominent than primary lateral veins on both surfaces, 2–7 mm from margin. *Inflorescences* shorter than leaves; peduncle (4)10–26 cm long, ca. 5 mm diam., 0.5–2× as long as petiole; spathe subcoriaceous, presumably lanceolate, more than 6 cm long, ca. 1.7 cm wide, decurrent at base; stipe ca. 2.7 cm long in front, 4 mm long in back; spadix color unknown, long-tapered to ± cylindroid in small plants, weakly curved, held at 160° angle from peduncle, 7.5–19.5 cm long, 9 mm diam. near base, 4 mm diam. near apex; flowers rhombic, 2.1–2.4 mm long, 1.4–1.7 mm wide, the sides straight to smoothly sigmoid; 9–11 flowers visible in principal spiral, 5–6 in alternate spiral; tepals roughened; lateral tepals 0.9–1.5 mm wide, the inner margins straight to broadly convex, the outer margins 2-sided; stigma linear, 0.5–0.7 mm long; anthers pale yellow, 0.5–0.6 mm long, 0.7–0.8 mm wide, obscuring the pistil; thecae oblong, slightly divaricate. *Infructescence* appearing to be ± erect; spathe deciduous; spadix ca. 21 cm long, 2 cm diam., reddish brown (excluding tepals); berries bright pinkish purple, oblong-ovoid, probably acute and with radial ridges at apex, becoming sunken in on drying, 7.5–8 mm long, 4.6–5 mm diam.; pericarp thickened, with numerous raphide cells; seeds 2 per berry, reddish brown, ± ovoid, flattened, 3.4–3.6 mm long, 2.2–2.4 mm diam., 0.8–1 mm thick, with a gelatinous, translucent, amber appendage at each end.

Anthurium solomonii is known only from La Paz Dept. in Bolivia at 1,000 to 1,400 m in wet subtropical or wet lower montane subtropical forest life zones (according to the Holdridge Life Zone Map for Bolivia).

This species is distinctive, with its spadix longer than the peduncle, a character otherwise known in the section only in *Anthurium plowmanii*. The petiole of *A. plowmanii* is narrowly sulcate adaxially with blunt margins, whereas in *A. solomonii* there is a prominent medial rib adaxially and prominently raised, acute margins. In Bolivia, *A. plowmanii* is known only from Pando and Santa Cruz departments and occurs at less than 900 m, mostly less than 300 m.

The species is named in honor of James Solomon, who has collected extensively in Bolivia and was involved in making all known collections of *A. solomonii*.

BOLIVIA. LA PAZ: Prov. Murillo. Valle de Zongo, 45 km below the dam at Lago Zongo, Cahua hydroelectric plant, 1,200–1,400 m, 16°3′S, 68°1′W, *Solomon 13000* (MO); Prov. Nor Yungas, Yolosa–Caranavi, 32.1 km N of Yolosa, 1,000 m, 16°2′S, 67°39′W, *Solomon & Escobar 12494* (LPB, MO); 10 km by road N and above Caranavi, 1,400 m, 15°47′S, 67°32′W, *Nee & Solomon 30311* (NY).

Anthurium soukupii Croat, sp. nov. TYPE: Peru. Cuzco: Urubamba, Machupicchu, 0.5 km N of the union of Río Sayacmarca and Río Aobamba, 2,370 m, *Peyton & Peyton 1486*

(holotype, MO 3024625-6). Figures 294, 297, 298.

Planta terrestris; caulis elongatus, ad 50 cm longus; internodia 1.5–2.5 cm diam.; cataphyllum lanceolatum, persistens in fibris linearis; petiolus 6.5–11 cm longus, ca. 5–7 mm diam., triangularis; lamina late ad anguste oblanceolato-elliptica, (22.5)28–63 cm longa, (3.8)4.7–10 cm lata; pedunculus 22–40 cm longus, 2–4 mm diam.; spatha lanceolata, 4.5–8 cm longa, 7–14 mm lata; spadix atropurpureus leviter contractus, 3.5–6 cm longus, ca. 4–5 mm diam.; baccae globosae, 3.2–4 mm longae.

Terrestrial; stem elongate, to 50 cm long, 1.5–2.5 cm diam.; roots moderately numerous, dense, white, smooth, thick, ± elongate; cataphylls lanceolate, probably subcoriaceous, to 11 cm long, acute at apex, drying yellowish tan, persisting as fine linear fibers. *Leaves* spreading; petioles 6.5–11 cm long, ca. 5–7 mm diam., triangular, flattened adaxially with the margins moderately to sharply raised, sides weakly convex, obtusely rounded to acutely angular abaxially; geniculum not at all or only slightly thicker than petiole when dried, 0.7–1 cm long; blades coriaceous, broadly to narrowly oblanceolate-elliptic, acute at apex, acute to obtuse at base, (22.5)28–63 cm long, (3.8)4.7–10.7 cm wide, broadest above the middle, the margins straight to weakly undulate; upper surface semiglossy, medium green, paler below; both surfaces drying matte, occasionally semiglossy below, green to yellowish; midrib convex- to round-raised above, sharply acute below; primary lateral veins numerous, to more than 20 per side, departing midrib at 50–65° angle, ± straight, obscure to raised and darker than surface above, flat to weakly raised below; interprimary veins numerous, almost as conspicuous as primary lateral veins on both surfaces; tertiary veins not visible on either surface; collective vein arising from near the base, sometimes in the upper third of the blade, equally as prominent as primary lateral veins on both surfaces when dried, 3–12 mm from margin. *Inflorescences* erect to spreading; peduncle 22–40 cm long, 2–4 mm diam., 2.6–4.2× as long as petiole, apparently ribbed abaxially; spathe reflexed, subcoriaceous, green, lanceolate, 4.5–8 cm long, 0.7–1.4 cm wide, broadest near the base, acuminate at apex, acute at base; stipe to 1 cm long in front, to 3 mm long in back; spadix dark purple, weakly tapered, stipitate to sessile, ca. 3.5–6 cm long, ca. 4–5 mm diam. near base; flowers ± square 3.1–4.3 mm in both directions, the sides straight to smoothly sigmoid; 5–6 flowers visible in principal spiral, 6–7 in alternate spiral; lateral tepals 2.3–3 mm wide, the inner margins straight, slightly turned up against the pistil, the outer margins 2-sided; pistils drying blackened, emergent well above the tepals, green; stigma linear, 0.5–0.6 mm long; anthers pinkish, ca. 0.8 mm long, 1 mm wide; thecae ovoid, slightly divaricate. *Infructescence* with spathe absent; spadix 3–13.5 cm long, 0.8–1 cm diam.; berries globose, rounded at apex, 3.2–4 mm long, 3.7–4.5 mm diam.; pericarp thickened, with numerous pale raphide cells; mesocarp translucent, gelatinous; seeds 2 per berry, reddish brown, ovoid, flattened, dried 3–3.5 mm long, 2.3–2.4 mm diam., 1.1–1.3 mm thick, enveloped by gelatinous, sticky, amber substance.

A member of series *Multinervia*, *Anthurium soukupii* ranges from La Paz in Bolivia to Zamora–Chinchipe in Ecuador, at (1,700) 2,000 to 2,400 m in subtropical lower montane moist forest, lower montane wet forest, subtropical montane wet forest, and high montane wet forest life zones.

This species is characterized by its elongate stem, subtriangular petiole, oblanceolate-elliptic blades with more than 20 primary lateral veins and a collective vein arising from near the base, and by its slightly tapered, purple spadix with 5–6 flowers per spiral.

It is probably most easily confused with *Anthurium fasciale*, also from the Atlantic slope in southern Ecuador. That species, in addition to occurring at elevations below 1,600 m, differs in having 8–11 flowers visible per spiral and pistils which dry yellow-brown, lack raphide cells on the surface and are round (not at all protruding) at the apex.

Anthurium soukupii may also be confused with *A. penningtonii*, another species from the Atlantic slope, but the latter differs in having more broadly elliptic blades with the primary lateral veins sharply elevated. There is an even closer resemblance between *A. soukupii* and *A. angustilaminatum*, from the Pacific slope. See that species for a discussion of the differences.

The new species is named in honor of Jaroslav Soukup, author of a book on vernacular names of Peruvian plants and the first to collect *A. soukupii*.

BOLIVIA. COCHABAMBA: Prov. Chapare, San Onafre, 1,700 m, *Steinbach 9419* (GH). LA PAZ: Prov. Sud Yungas, Huancane, 13 km toward San Isidro, N of Chulumani, 2,200 m, *Beck 8756* (MO). ECUADOR. ZAMORA–CHINCHIPE: Loja–Zamora, 13 km E of Loja, 2,220 m, 4°5′S, 79°6′W, *Croat 50747* (CM, MO). PERU. AMAZONAS: Prov. Bongara, Lago Pomacocha, Moyobamba–Pomacocha, Km 340, 2,200 m, 5°47′S, 77°53′W, *Croat 58298* (CM, MO, RSA, USM). CAJAMARCA: Prov. Santa Cruz, Dtto. Catache, upper Río Zaña valley, ca. 5 km above Monte Seco on path to Chorro Blanco, 1,500–2,000 m, *Dillon et al. 4385A, 4905* (F, MO); Prov. Cutervo, Parque Nacional de Cutervo, 2,300–2,400 m, *Díaz et al. 3964*

(MO). CUZCO: Río Lucumayo, La Convención, 6 km from Incatambo, 2,350 m, *Peyton & Peyton 994* (MO); Prov. Urubamba, 2,100 m, *Nuñez 8928* (MO); Machupicchu, on slope 0.5 km N of confluence of Río Sayacmarca and Río Aobamba, 2,370 m, *Peyton & Peyton 1486* (MO); 2.5 km from Machupicchu, above 1st waterfall of Río Mandor, 2290 m, *Peyton & Peyton 455* (MO). JUNÍN: Prov. Oxapampa, *Soukup 2324* (GH). PASCO: Cordillera Yanachaga, trail to summit of Cordillera via Río San Daniel, 2,400 m, 10°23′S, 75°27′W, *Smith et al. 7929* (MO).

Anthurium sparreorum Croat, sp. nov. TYPE: Ecuador. Los Ríos: Centro Cientifico Río Palenque, W of laboratory & vic. of laboratory clearing, 210–250 m, *Croat 38666* (holotype, MO 2387864-65; isotypes, B, CAS, CM, K, M, NY, QCA, RSA, US). Figures 12, 19, 299, 300–302.

Planta plerumque epiphytica, subinde terrestris; cataphyllum late lanceolatum, persistens semi-intactum, demum in reticulum fibris tenuis; petiolus (11.5)15–38 cm longus, 6–15 cm diam., D- ad U-formatus complenatus ad sulcatus ad leviter sulcatus; lamina oblongo-elliptica ad anguste oblanceolata ad oblongo-lanceolata, 46–96 cm longa, (9.5)15–25 cm lata; pedunculus 11–34 cm longus, 5–10 mm diam.; spatha lanceolata vel ovata, (9)12–16 cm longa, 2.8–4.5 cm lata; stipes 5 mm longus; spadix atropurpureus ad violaceus, cylindricus, 5.8–20 cm longus, 8 mm diam.; baccae rubrae.

Usually epiphytic, occasionally terrestrial; stem short and thick, 5.5–15 cm long, 2.5–5 cm diam.; roots numerous, descending, bright green to greenish white, densely pubescent, elongate, 3–5 mm diam.; cataphylls subcoriaceous, broadly lanceolate, conspicuously 1-ribbed, 9–18 cm long, acute at apex with subapical apiculum, green, drying pale yellow-tan (B & K yellow-red 9/7.5), persisting semi-intact, eventually dilacerating into reticulum of fine fibers. *Leaves* erect to spreading; petioles (11.5)15–38 cm long, 6–15 mm diam., D- to U-shaped, flattened and sulcate to weakly convex with the margins bluntly to sharply raised adaxially, rounded to 1–3-ribbed abaxially, the surface densely pale-speckled; geniculum thicker and paler than petiole, 1–2.5 cm; blades coriaceous, oblong-elliptic to narrowly oblanceolate to oblong-lanceolate, acuminate to obtuse-rounded at apex (the acumen weakly apiculate), acute to obtuse or cuneate at base, 46–96 cm long, (9.5)15–22 cm wide, broadest at or near the middle, the margins slightly undulate; upper surface matte to semiglossy, medium to dark green, lower surface glossy to semiglossy, paler; both surfaces drying matte, green to pale yellow; midrib above prominently convex at base, becoming 1-ribbed toward the apex, paler than surface and somewhat speckled, below obtusely raised at base, becoming prominently convex toward the apex and paler than surface, drying convex on both surfaces; primary lateral veins (15)20–30 per side, departing midrib at 40–70° angle, straight or arcuate, prominently convex and paler than surface above, less convex to flat and slightly darker than surface below; interprimary veins almost as conspicuous as primary lateral veins, raised above, flat to weakly raised below; tertiary veins obscure above and below, slightly raised when dried on both surfaces; collective vein arising from near the base, occasionally in the upper third of the blade, weakly sunken and less prominent than primary lateral veins above, raised and equally as prominent as primary lateral veins below, 4–15 mm from margin. *Inflorescences* erect to erect-spreading to spreading, shorter than leaves; peduncle 11–34 cm long, 5–10 mm diam., 0.5–2× as long as petiole, medium green, terete, sometimes 1-ribbed below the spathe; spathe reflexed-spreading, slightly twisted, subcoriaceous, green (B & K green 6/2.5), broadly to narrowly lanceolate or ovate, 9–16 cm long, 2.8–4.5 cm wide, broadest near the base, inserted at 60° angle on peduncle, acuminate at apex (the acumen inrolled), obtuse at base, the margins meeting at 110° angle; stipe 7–10 mm long in front, to 5 mm long in back; spadix dark purple to reddish violet (B & K purple 3/2.5), cylindroid to short-tapered at apex, ± erect, 5.8–20 cm long, ca. 8 mm diam. near base, 4–5 diam. near apex; flowers irregularly 4-lobed to rhombic, 1.8–2.6 mm long, 1.8–2.8 mm wide, the sides jaggedly sigmoid to straight; 9–13 flowers visible in principal spiral, 8–10 in alternate spiral; tepals matte, densely and minutely punctate and papillate; lateral tepals 1–1.2 mm wide, the inner margins straight; pistils scarcely emergent, glossy, papillate, with exposed portion ± rectangular, green; stigma linear, dark purple, 0.4–0.6 mm long; stamens emerging ± regularly and promptly from the base, laterals emerging throughout, or at least to midway, before alternates emerge, borne at the edge of tepals; filaments translucent to greenish, minutely purple-spotted, soon retracting, 0.9 mm wide; anthers pale orange with purple punctations, 0.5–0.7 mm long, 0.7–0.8 mm wide; thecae oblong-ovoid, scarcely divaricate; pollen bright orange fading to lavender or pinkish white, faintly yeasty-scented. *Infructescence* with spathe persisting; spadix 20–22 cm long, ca. 2 cm diam.; berries red, exserted slightly beyond the tepals, subglobose, ca. 5 mm diam.; tepals becoming fleshy, white, enlarged, elongate and 3-sided in cross section with the outer angle of the apex raised and acute.

Anthurium sparreorum is nearly restricted to the Province of Los Ríos in Ecuador, at 210 to 250 m in a tropical moist forest life zone. An additional collection is known from Cotopaxi.

This species is characterized by its short stem, dense, bright green to greenish white roots, cataphylls drying pale yellow-tan and persist semi-intact, coriaceous leaf blades drying matte and green and reddish violet, cylindroid spadix. Most significant is the infructescence, with the berries exserted beyond the tepals. The latter become fleshy, whitish, enlarged and elongated, with the outer edge raised and acute.

Anthurium sparreorum bears some resemblance to both *A. campii* and *A. bucayanum*, which also have large, green-drying leaves with the collective vein arising from near the base. *Anthurium campii* differs in its green spadix, more coriaceous leaf blades, and shorter petioles. *Anthurium bucayanum* differs in its very thin leaves and prominently stipitate spadix. *Anthurium sparreorum* also has a shorter peduncle than either of these species.

The new species is named in honor of the late Benkt Sparre, formerly curator of the Regnellian Herbarium in Stockholm and co-editor of the Flora of Ecuador Project, and his wife, Bride. Together they made concentrated efforts to collect Araceae and discovered numerous novelties in the process.

ECUADOR. Cultivated by Tom Fennel, Homestead, Florida, *Croat 57195* (F, MO). COTOPAXI: Río Guapara, 20 km NW of El Corazón, 250 m, *Sparre 17248* (S). LOS RÍOS: Río Palenque Biological Station, Quevedo–Santo Domingo, 210–250 m, *Croat 38666* (B, CAS, CM, K, M, MO, NY, QCA, RSA, US), *Dodson & Tan 5389* (US, SEL), *Madison 3715* (SEL), *5513* (K), *6959* (MO, SEL, US).

Anthurium spathiphyllum N. E. Br., Gard. Chron. I. 652. 1877. TYPE: Origin unknown, Hort. Kew, 8 Nov. 1876 (holotype, K). Figures 303, 304.

Epiphytic; stem ca. 10 cm long, 2 cm diam.; roots moderately numerous, descending, greenish gray, prominently pubescent, gradually tapered and elongate, 3–5 mm diam.; cataphylls subcoriaceous, lanceolate, 6–8 cm long, cuspidate at apex with subapical apiculum ca. 15 mm long, green, drying pale tan (B & K yellow 9/7.5), persisting as linear fibers. *Leaves* spreading; petioles 6–26 cm long, 5–8 mm diam., triangular, sometimes 3–5-ribbed or flattened with the margins prominently raised adaxially, sharply 1–2-ribbed abaxially; geniculum conspicuously thicker and slightly paler than petiole, 0.7–1 cm long; blades subcoriaceous, linear to narrowly oblong-elliptic or narrowly oblong-oblanceolate, more than 5× longer than wide, acuminate at apex (the acumen apiculate), narrowly acute at base, 46–80 cm long, 5.5–12.5 cm wide, broadest at or above the middle, the margins broadly undulate; upper surface matte to glossy, dark to medium green, lower surface matte to weakly glossy, paler below; midrib flat at base, becoming angular-raised toward the apex above, prominently and sharply raised and slightly paler than surface below; primary lateral veins 20–30 per side, departing midrib at 40–45° angle, straight to the collective vein, deeply sunken above, sharply raised below; interprimary veins almost as conspicuous as primary lateral veins, sunken above, raised below; tertiary veins obscure above, raised and slightly darker than surface below; collective vein arising from near the base, sunken above, sharply raised below, equally as prominent as primary lateral veins, 3–10 mm from margin. *Inflorescences* spreading, shorter than leaves; peduncle 33–48 cm long, 4–15 mm diam., 2× as long as petiole, green, prominently 2-winged-angled on one side, rounded to sharply acute on the other (or triangular or few-angled near base); spathe erect, hooded over the spadix, subcoriaceous, green, lanceolate to broadly lanceolate, 6.5–8 cm long, 1.7–3 cm wide, broadest near the base, about twice as long as spadix, inserted at 50° angle on peduncle, acuminate at apex (the acumen apiculate, 4 mm long), obtuse to rounded at base; spadix pale yellow to creamy white, cylindroid to clavate, short and stubby, erect, (1.7)2–4 cm long, 6–11 mm diam.; flowers 1.8–2.2 mm long, 1–1.2 mm wide, the sides smoothly to jaggedly sigmoid; 7–12 flowers visible in principal spiral, 11–15 in alternate spiral; tepals matte, densely and minutely papillate; lateral tepals 0.7–0.8 mm wide, the inner margins straight to convex, the outer margins irregularly 2–4-sided; pistils somewhat emergent, matte, pale yellow; stigma linear, 0.1–0.2 mm long; stamens emerging in a scattered pattern throughout, lateral stamens almost to apex before alternates emerge, inclined over and obscuring pistil; filaments fleshy; thecae oblong, not divaricate; pollen pale yellow fading to creamy white. Berries translucent white.

Anthurium spathiphyllum is known from Nicaragua to Panama mostly from sea level to 380 m (rarely to as high as 1,350 m) on the Atlantic slope in wetter parts of tropical wet forest and in premontane wet and tropical wet forest life zones.

Anthurium spathiphyllum can be recognized by its epiphytic habit, chartaceous leaves, usually triangular, sometimes three- to five-ribbed petiole,

lanceolate to broadly lanceolate, cucullate spathe, and short, scarcely tapered, pale yellow spadix.

Anthurium spathiphyllum can be confused with *A. bradeanum*, which has a similarly clavate spadix, but that species has oblanceolate-elliptic blades less than five times longer than wide (vs. more than five in *A. spathiphyllum*), with (5)10–15 pairs of primary lateral veins that are not deeply impressed, a peduncle which is not prominently winged, a deflexed, ovate spathe about as long as the spadix, and petioles that are commonly quadrangular in cross section.

COSTA RICA. ALAJUELA: 3 mi. N of San Miguel, 380 m, *Croat 35651* (MO, RSA). HEREDIA: 4 mi. N of Vara Blanca, 1,350 m, *Croat 35571* (MO); Finca La Selva, OTS Field Station on Río Puerto Viejo, just E of its junction with Río Sarapiquí, 100 m, *Wilbur & Jacobs 34194* (DUKE), *Folsom 8950* (CAS); Puerto Viejo de Sarapiquí, along El Surá trail, 100–150 m, *Croat 44309* (MO); Puerto Viejo Region, Río Puerto Viejo, *Burger & Mata 4258* (F); Zona Protectora La Selva, 6 km by road from Río Peje crossing, 5 km SSE of Magsasay, 10°21′N, 84°4′W, 340 m, *Schatz & Grayum 644* (DUKE). LIMÓN: Pandora, 100 m, *Ocampo 1987* (MO); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8954* (MO); Quebrada Mata de Limón headwaters, Finca Anai, Sixaola, 25–40 m, 9°35′N, 82°39′W, *Grayum 4515* (MO); Río Parismina, W of Dos Bocas, *Lent 2444* (F); Talamanca, Cocles, 150 m, *Ocampo 1906* (MO). PUNTARENAS: Parque Nacional Corcovado, campamento Sirena, *Téllez et al. 4248* (MEXU, MO). SAN JOSÉ: Parque Nacional Braulio Carrillo, Fila Carrillo, 600–700 m, *Chacón 338* (MO); Chasse, Talamanca, 200 m, *Ocampo 1625* (CR); 300 m, *Ocampo 1624* (CR). NICARAGUA. ZELAYA: 0.3–1.9 km N of Limbaika, 8–10 m, 13°29′N, 84°13′W, *Stevens 8255* (MO); Risco de Oro, 40 m, *Pipoly 5021* (MO); Colonia Kururia, 50 m, 14°41′N, 84°4′W, *Pipoly 3968* (MO); 13 km above Kururia, on road to San Jerónimo, 200 m, 14°39–42′N, 84°4–11′W, *Pipoly 3743, 3830* (MO); Rosita–Puerto Cabezas, 15.7 km SW of Río Kukalaya, 100 m, 13°58′N, 84°12′W, *Stevens 8504* (MO). PANAMA. BOCAS DEL TORO: Changuinola–Almirante, Milla 7.5, above RR stop, *Croat & Porter 16276* (MO), *Kennedy 1273* (DUKE); 15 km S of Changuinola, 300 m, *Antonio 3150* (MO); Almirante–Changuinola Canal, *Blum 1403* (FSU, SCZ). COCLÉ: at confluence of Río Toabre and Río Coclé del Norte, Boca del Toabre, *Lewis et al. 5569* (MO).

Anthurium spectabile Schott, Oesterr. Bot. Z. 8: 181. 1858. TYPE: Costa Rica. Cartago: Volcań Turrialba, *Wendland 506* (holotype, GOET). Figures 305, 319.

Anthurium longispathum Schott, Prodr. Aroid. 520. 1858. TYPE: Costa Rica. Turrialba, *Oersted s.n.* (lectotype, illustrated by Schott Aroideae 707).

Epiphytic; stem erect; cataphylls coriaceous, 17–51 cm long, lanceolate, obtuse to mucronate at apex, light green, drying light tan (B & K yellow-red 9/10), persisting with the apex remaining intact. *Leaves* spreading; petioles 14–63 cm long, 7–12 mm diam., quadrangular, flattened to broadly and sharply sulcate adaxially, the margins sharply raised, sharply 2–3-ribbed abaxially; geniculum thicker and paler than petiole, becoming fissured transversely with age, (1.3)2–7 cm long; blades coriaceous, oblong-lanceolate to oblong or oblong-triangular, rounded to obtuse to acuminate at apex, rounded to truncate at base, 37–140(160) cm long, 8–38(45) cm wide, the margins undulate; upper surface matte to semiglossy, medium green, lower surface semiglossy to glossy, paler; midrib obtusely angular at base, becoming narrowly raised toward the apex above, prominently higher than broad at base, becoming prominently convexly raised toward the apex below, paler than surface above and below; primary lateral veins more than 20 per side, departing midrib at 45–75° angle, prominently and narrowly raised above and below; tertiary veins obscure above, raised and darker than surface below; collective vein arising in the lower half of the blade, sunken above, raised below, less prominent than primary lateral veins, 2–3 mm from margin. *Inflorescences* spreading, shorter than leaves; peduncle 13–25 cm long, 0.6–0.7× as long as petiole, terete; spathe usually recurled and twisted, prominently reflexed, subcoriaceous, green or violet-purple, narrowly ovate to oblong-lanceolate, 10.5–32 cm long, 3–7 cm wide, inserted at 45° angle on peduncle, acuminate at apex, rounded to subcordate at base; spadix yellow-green, long-tapered, 16–38 cm long, 9–12 mm diam. near base, 6–7 mm diam. near apex; flowers rhombic to 4-lobed, 2.5–4 mm in both directions, the sides sigmoid; 7–11 flowers visible in principal spiral, ca. 9 in alternate spiral; tepals matte to semiglossy; lateral tepals ca. 2.7 mm wide, the inner margins convex; pistils emergent, green, violet-purple at apex; stigma ellipsoid, ca. 1 mm long, stamens emerging promptly throughout length of spadix in a complete sequence, grouped in a circle around the pistil; anthers 1–1.1 mm long, 1–1.2 mm wide; thecae oblong to narrowly ovoid, slightly divaricate; pollen cream. *Infructescence* with spadix to 50 cm long; berries probably orange at maturity, oblong-linear, acute to blunt at apex, 10–14 mm long, ca. 3.5 mm diam.; seeds 2 per berry, 3.4–3.6 mm long, ca. 1.6 mm diam., with a minute appendage at both ends.

Anthurium spectabile is endemic to Costa Rica, where it occurs at 300 to 1,300 m in premontane wet forest and tropical wet forest life zones.

This species is recognized by its elongate, pen-

dent leaf blades with numerous, prominent primary lateral veins and erect, four-sided petioles. Also distinctive are the short peduncle, large, narrowly ovate, often violet-purple spathe, and yellow spadix.

Anthurium spectabile might be confused with *A. ranchoanum*, which has similar leaves (in dried herbarium material) and a similar inflorescence. *Anthurium ranchoanum*, however, has a subterete petiole and a more or less erect leaf blade in line with the petiole. *Anthurium spectabile* also has an elongate, more or less spreading spathe, while the spathe of *A. ranchoanum* is shorter and usually stiffly erect and hooding the spadix.

Anthurium spectabile is extremely similar to *A. pseudospectabile* from Panama, but the latter has proportionally longer blades with more undulate margins, terete petioles, and occurs in premontane rainforest.

COSTA RICA. ALAJUELA: Cariblanco, *Lent 3543* (F); NE of Villa Quesada, *Molina et al. 17287* (F); Naranjo–Aguas Zarcas, Hwy. 15, 8.5 km NE of Villa Quesada, 600 m, *Croat 46968* (F, K, M, MO, NY, RSA, SEL); Río Sarapiquí at bridge on road to Colonia Virgen del Socorro, 830 m, *Croat 68303* (MO). HEREDIA: Río Guacimito, Magsasay, 500 m, *Chacón 167* (MO); Río Peje–Río Sardinalito, Atlantic slope of Volcán Barva, 700–800 m, 10°17.5′N, 84°04.5′W, *Grayum 6719* (MO). LIMÓN: Turrialba–Limón, 11 mi. S of Siquirres, Hwy. 32, 650 m, *Croat 43325* (MO); Guápiles, *Smith 4982* (US); road from Río Frío to Limón, vic. of Río Blanco, W of Guápiles, 360 m, 10°12′N, 83°49′W, *Croat 68428* (MO); Zona Protectora, Barbilla (SE of Squirres), 600–660 m, 10°0′N, 83°28′W, *Grayum et al. 7939* (CR, MO). PUNTARENAS: cultivated at Las Cruces Botanical Garden, 1,300 m, *Croat 44431* (MO). SAN JOSÉ: Carrillo Station, *Gómez et al. 21188* (MO).

Anthurium standleyi Croat & R. A. Baker, Brenesia 16(Suppl. 1): 88. 1979. TYPE: Costa Rica. San José: ca. 5 mi. SW of Canaán along gravel road from Rivas, ca. 900 m, *Croat 43439* (holotype, MO 2582987; isotypes, COL, CR, DUKE, F, K, LE, MEXU, NY, PMA, SEL, US, VEN, W). Figures 306, 307, 320.

Terrestrial; stem to 90 cm long, 2–5 cm diam.; roots descending, greenish to tan, smooth to fuzzy, slightly tapered, 4–12 mm diam.; cataphylls moderately coriaceous, lanceolate, 13.5–30 cm long, obtuse at apex with subapical apiculum, light green, drying tan (B & K red 9/10), persisting semiintact, eventually as linear fibers. *Leaves* erect to spreading; petioles 43–120 cm long, 7–16 mm diam., stiff, firm, terete to subterete, sometimes weakly flattened adaxially, surface minutely pale-speckled; geniculum slightly thicker and paler than petiole, 3.5–6.5 cm long; blades subcoriaceous, ovate to ovate-triangular, acuminate at apex (the acumen apiculate, downturned), cordate at base, 29–75 cm long, 19–56 cm wide, broadest at the point of petiole attachment or slightly above it, the margins conspicuously undulate; anterior lobe 23–55 cm long; the posterior lobes 7–21 cm long; sinus spathulate to obovate, often closed with the lobes overlapping, 3.5–12 cm deep, the inner edges turned up; upper surface weakly glossy to semiglossy or matte, dark green, lower surface semiglossy to matte, slightly paler; midrib triangular-raised at base, becoming sharply and narrowly raised toward the apex above, prominently and convexly raised and paler than surface below; basal veins 4–6 pairs, 4–5 coalesced 1–4 cm, two lowermost sunken, others raised above, convexly raised below; posterior rib slightly curved, naked, sharply turned up on the outer margin; primary lateral veins 4–9 per side, departing midrib at 45–80° angle, straight, becoming arcuate-ascending, usually only the uppermost loop-connected, convexly raised above and below, prominently raised below on drying; interprimary veins obscure or occasionally raised in grooves above, raised below; tertiary veins obscure above, slightly darker than surface below; reticulate veins slightly raised on both surfaces on drying; collective vein arising from about the middle of the blade, slightly sunken above, raised and slightly darker than surface below, slightly raised above and below on drying, 4–11 mm from margin. *Inflorescences* erect to spreading, much shorter than leaves; peduncle 29–76 cm long, 4–9 mm diam., 0.3–0.8× as long as petiole, green, terete; spathe erect-spreading to reflexed, subcoriaceous, green to yellow-green (B & K yellow-green 6/7.5), oblong-lanceolate, 10.5–18 cm long, 2–4 cm wide, broadest just above the base, inserted at 60–80° angle on peduncle, narrowly acuminate at apex (the acumen inrolled and hooked), obtuse to rounded at base, the margins meeting at 90–180° angle; stipe 11–70 mm long in front, 6–60 mm long in back; spadix heavily tinged with violet-purple at anthesis, becoming yellowish brown, long-tapered, 10–30 cm long, 7–10 mm diam. near base, 4–6 mm diam. near apex; flowers rhombic to weakly 4-lobed, 3.5–3.6 mm long, 2.9–3.3 mm wide, the sides ± straight to smoothly sigmoid; 5–10 flowers visible in principal spiral, 5–7 in alternate spiral; tepals semiglossy; lateral tepals 1.9–2 mm wide, the inner margins broadly convex; pistils weakly raised, medium green; stigma linear at anthesis, 0.4–0.7 mm long, droplets appearing before stamens emerge; stamens emerging from the base in

prompt sequence; anthers orange to greenish yellow, 0.6–1 mm long, ca. 1 mm wide, inclined over and obscuring the pistil; thecae ellipsoid, not divaricate; pollen orange fading to creamy white. *Infructescence* arching; spathe reflexed; spadix to 30 cm long, ca. 2 cm diam.; berries orange, broadly ovoid, rounded at apex; mesocarp pulpy, bitter-tasting; seeds 1 or 2 per berry, white, to 5 mm long, ca. 2.5 mm wide, 1.5 mm thick.

Anthurium standleyi is known for certain only from central and southern Costa Rica. It was first collected by Paul Standley at two sites, La Verbena and San Sebastian south of San José in what was probably premontane wet forest. It has been collected more recently in the region northeast of San Isidro del General. The species ranges from 200 to 1,600 m and may be restricted to premontane wet forest.

This species is distinguished by its cordate leaf blades, long-tapered, purplish violet spadix and orange berries. Among Central American species with cordate leaf blades and orange fruits, *A. standleyi* is unique in having an ovate leaf blade and a collective vein originating above the middle of the blade.

Because of its prominently cordate leaf blades, *Anthurium standleyi* is likely to be confused only with *A. watermaliense*, which differs in having the collective vein arising from the first or second basal vein and a proportionally broader, often maroon spathe.

A cultivated collection from the University of Hawaii was reportedly based on a Dressler collection from Achiote, a region of tropical moist forest in the Isthmus of Panama. The species has never been collected in Panama, and the Hawaiian collection is possibly mislabeled.

COSTA RICA. PUNTARENAS: Río Coto Brus, 23 km N of La Unión, Panama border, *Croat 26674* (MO); cultivated at Las Cruces Botanical Garden, 1,300 m, *Croat 44436* (MO). SAN JOSÉ: Santa Eduviges de Escazú, residential neighborhood at W side of Rte. 105, 1,150 m, 9°55′N, 84°08.5′W, *Grayum 9510* (CR, MO); 0.5 mi. above turnoff to Canaán at Rivas, 900 m, *Croat 43431* (MO); 4.5 mi. SW of Canaán, road from Rivas, 900 m, *Croat 43439* (B, CAS, COL, CR, DUKE, F, GH, HUA, K, LE, M, MEXU, MO, NY, PMA, QCA, RSA, SEL, UC, US, VEN, W); La Verbena, *Standley 32243* (US); San Sebastián, *Standley 49296* (US); Talamanca, less than 200 m, *Tonduz 8721* (NY); Cerro Tapezco, *Jiménez 627* (US); Río Buena Vista, S of Buena Vista, NE of San Isidro del General, *Luteyn 3287* (DUKE); Río Herradura (tributary of Río Chirripó del Pacífico), NW of Canaán, Valle General, 1,600 m, 9°29′N, 83°37′W, *Burger & Liesner 7093* (MO, US).

Anthurium superbum Madison, Selbyana 5: 94. 1978.

a. Anthurium superbum subsp. **superbum**. TYPE: Ecuador. Napo: La Primavera, Río Napo, *Madison 5516* (holotype, SEL 2727370; isotypes, F, K, MO, QCA, U, US). Figures 308, 309.

Epiphytic; stem 4–8 cm long, 3–4 cm diam.; roots numerous, descending, rose-colored, velutinous, 5–7 mm diam.; cataphylls subcoriaceous, (3)8–10 cm long, acute at apex, dark green, drying brown, persisting intact or semi-intact. *Leaves* erect; petioles 4–12 cm long, 5–8 mm diam., ± D-shaped, with the medial rib and the margins raised adaxially, 3–5-ribbed to rounded abaxially, the surface dark green to sometimes dark purple-green; geniculum slightly thicker than petiole, ca. 0.8 cm long; blades coriaceous, stiff, elliptic to oblong-elliptic, obtuse-rounded at apex, obtuse at base, 34–65 cm long, 12–18 cm wide, broadest just above the middle, the margins revolute; upper surface matte to semiglossy, bullate, dark green, lower surface matte, sometimes tinged reddish or purple; midrib prominently acute above and below; primary lateral veins 7–10 per side, departing midrib at 40–50° angle, very long-arcuate to the margin or slightly arcuate to the collective vein, sunken to weakly raised above, raised below, drying slightly raised above and below; interprimary veins few, less prominent than primary lateral veins; tertiary veins sunken above, raised below, drying slightly raised; collective vein arising from about the middle of the blade or absent, sunken above, raised below, slightly raised above and below when dried, nearly as prominent as primary lateral veins, 10–20 mm from margin. *Inflorescences* erect, shorter than leaves; peduncle 7–18 cm long, 5–12 mm diam., ca. 2× as long as petiole, dark green, terete; spathe spreading to reflexed, subcoriaceous, green, lanceolate-elliptic, 8–9 cm long, 2–3 cm wide, broadest near the base, acute at apex (the acumen slightly inrolled), acute at base; stipe to 5 mm long; spadix creamy white, sometimes faintly tinged with purple, cylindroid, sessile or shortly stipitate, erect, straight to slightly curved, 8–15 cm long, 8–12 mm diam. midway; flowers ± rhombic, 1–1.5 mm long, 1.5–2 mm wide; 16–17 flowers visible in principal spiral, 23–24 in alternate spiral; tepals minutely puberlent to densely papillate; lateral tepals 0.7–0.9 mm wide, inner margins ± straight, outer margins 2–4-sided; pistils prominently exerted, papillate; stigma circular, 0.3 mm long, brushlike.

Infructescence with the spathe persisting; berries lavender with the apical ¼ white, obovoid, sharply apiculate at apex, 6–7 mm long, 2.5 mm diam.

Anthurium superbum is known to occur in tropical moist to tropical wet forest life zones, at 180 to 350 m. It comprises two allopatric subspecies, the typical one in Napo, Ecuador, near La Primavera on the Río Napo, and subsp. *brentberlinii* in Amazonas, Peru, in the Río Cenepa area. Both subspecies are characterized by their stiffly erect, dark green leaves with short petioles and bullate, coriaceous blades often tinged red or purple below, and by the short inflorescence with a whitish spadix with many flowers per spiral. Neither subspecies is likely to be confused with any other member of the section.

While subsp. *brentberlinii* is not known in cultivation, subsp. *superbum* has been cultivated for about 10 years in a few botanical gardens and by a few hobbyists. It is a stunning plant and will, hopefully, become more widespread in cultivation in the future.

ECUADOR. NAPO: Río Napo, La Primavera, *Madison 5516* (F, K, MO, QCA, SEL, U, US); Laguna Taracoa, 250 m, *Christenson 1529* (MO), cultivated.

b. Anthurium superbum subsp. **brentberlinii** Croat, subsp. nov. TYPE: Peru. Amazonas: Río Cenepa, E of community of Huampami, 300–330 m, *Berlin 644* (holotype, MO 2251387; isotype, NY). Figure 310.

Differt ssp. typicum caulibus longioribus, laminas angustioribus, spadice angustiore cum seriebus spiralibus paucioribus florum.

Epiphytic; stem to 16 cm long, 7–14 mm diam.; roots dense, 3–5 cm long, 3–4 mm diam.; cataphylls subcoriaceous, linear-lanceolate, 3–13 cm long, drying reddish brown, persisting semi-intact. *Leaves* erect; petioles 9–17 cm long, 5–10 mm diam., D-shaped, with the medial rib and margins raised adaxially, angular abaxially; geniculum somewhat darker than petiole when dried, 0.5–1 cm long; sheath 2.5–4 cm long; blades coriaceous, oblong-elliptic, acute to obtuse at apex, attenuate to acute at base, 45–70 cm long, 9–17 cm wide, broadest just above the middle; upper surface apparently quilted, lower surface often tinged red or purple; midrib acutely raised above and below; primary lateral veins 4–9 per side, departing midrib at 50–60° angle, very long-arcuate to the margin or slightly arcuate to the collective vein, raised to obscure above, raised below when dried; interprimary veins usually present, less conspicuous than primary lateral veins; tertiary veins weakly raised to obscure above and below when dried; collective vein arising from about the middle of the blade or absent, rarely from near the base, sunken above, raised below when dried, equally as prominent as primary lateral veins, 10–15 mm from margin. *Inflorescences* erect; peduncle 11–29 cm long, 2–5 mm diam., 1–2.6× as long as petiole, terete; spathe reflexed, subcoriaceous, green, oblong-lanceolate, 4–10 cm long, 1–2 cm wide, broadest near the base, acute at apex, acute at base; spadix white, cylindroid, ± straight, 5–7 cm long, 4–6 mm diam. midway; flowers ± rhombic, ca. 0.8 mm in both directions; ca. 12–15 flowers visible in either spiral; tepals densely papillate; stamens held erect above the tepals; filaments exserted 0.2 mm; anthers 0.2 mm in both directions. *Infructescence* spreading-pendent; spathe persisting or absent; spadix 20 cm long, 2 cm diam., with berries scattered throughout; berries purple, tipped white (B & K purple 5/5), obovoid-ellipsoid, obtuse at apex, ca. 7 mm long, ca. 4 mm diam.; pericarp with numerous raphide cells; seeds 1–2 per berry, yellow-brown when dried, oblong, 2 mm long, 1 mm diam.

Anthurium superbum subsp. *brentberlinii* is endemic to northern Peru in Amazonas, where it is known only from the Río Cenepa area at 180 to 350 m in a tropical wet forest life zone.

This subspecies is characterized by its slender, densely rooted stem, short petioles, oblong-elliptic leaf blades with steeply ascending primary lateral veins and often tinged red or purple below, and cylindroid, white spadix with very small flowers.

Anthurium superbum subsp. *brentberlinii* differs from the typical subspecies because of its narrower leaf blades, more slender stem, and more slender spadix with fewer flowers per spiral.

The new subspecies is named in honor of Brent Berlin (Department of Anthropology, University of California at Berkeley), who coordinated all known collections of this taxon.

PERU. AMAZONAS: Río Cenepa, Cenepa area, 250 m, *Kayap 1252* (MO); Cenepa–Quebrada Kayamas, 250 m, *Berlin 513* (MO); above Quebrada Shimpunts, 250–350 m, *Berlin 886* (MO); Huampami, 200–400 m, 4°30′S, 78°30′W, *Berlin 644* (MO, NY); *Kayap 2007* (MO), *Kujikat 162* (MO).

Anthurium tarapotense Engl., Pflanzenr. IV. 23B(Heft 21): 74. 1905. TYPE: Peru. San Martín: Tarapoto, *Ule 5p* (holotype, B). Figures 311, 312.

Terrestrial, occasionally epiphytic; stem short, 1.5–4 cm diam.; roots dense, spreading to descending, pale green, velutinous, short, tapered, 2–6 mm diam.; cataphylls lanceolate, subcoriaceous, 5–12 cm long, acuminate at apex, drying dark reddish brown, persisting semi-intact, eventually deciduous. *Leaves* erect to spreading; petioles 7–19 cm long, 3–10 mm diam., erect, sharply D-shaped, broadly convex to 1-ribbed to flattened or somewhat sulcate with the margins sharply raised or sharp but not raised adaxially, rounded to weakly 1-ribbed abaxially; geniculum moderately thicker and paler than petiole, becoming transversely fissured with age, 0.5–3 cm long; sheath 2–5 cm long; blades subcoriaceous to moderately coriaceous, broadly elliptic to broadly oblanceolate to oblanceolate, long-acuminate at apex (the acumen apiculate), long-attenuate to attenuate, rarely acute at base, (15)30–60(90) cm long, 8–27 cm wide, broadest near or above the middle, the margins undulate; upper surface weakly glossy to semiglossy, medium green (B & K green 2/2.5), lower surface semiglossy, conspicuously paler, both drying brown to greenish brown; midrib flat and 1-ribbed at base, becoming acutely angular toward the apex above, higher than broad at base, becoming obtusely angular and then convexly raised at apex below; primary lateral veins 5–10(16) per side, departing midrib at 40–80° angle, straight to less often arcuate to the margin, paler than surface, convexly raised above and below, more so above; tertiary veins obscure above, prominulous and darker than surface below; collective vein arising from about the middle of the blade, near the apex or absent, prominulous on both surfaces, to 12 mm from margin. *Inflorescences* erect to spreading; peduncle 23–50 cm long, 3–4 mm diam., 2–4.6× as long as petioles, yellowish green tinged with reddish in the lower half or purple, terete; spathe spreading to reflexed, subcoriaceous, concolorous with the petiole, sometimes tinged with purple or purple throughout, ovate-lanceolate to oblong-lanceolate, 4.5–15 cm long, 0.9–1.9 cm wide, inserted at 60° angle on peduncle, acuminate at apex (the acumen inrolled), rounded to obtuse at base; spadix purple to maroon (B & K red-purple 2/10) to yellowish green, sessile or stipitate to 5 mm, cylindroid to slightly tapered, erect to somewhat curved, (3)4–16 cm long, 4–6 mm diam. near base, 3–4 mm diam. near apex; flowers 4-lobed, 1.5–2.5 mm in both directions, the sides straight to jaggedly sigmoid; 4–6 flowers visible in principal spiral, 4–8 in alternate spiral; tepals matte, white-punctulate; lateral tepals 0.8–1.5 mm wide, the inner margins broadly rounded, the outer margins 2–3-sided; pistil weakly raised; stigma slitlike to ellipsoid, 0.4–0.6 mm long; stamens emerging irregularly, the laterals preceding the alternates by up to 16 spirals, the 3rd stamen preceding the 4th by 3–4 spirals, borne at edge of the tepals; anthers pinkish to reddish or orangish, 0.4–0.7 mm long, 0.6–0.8 mm wide; thecae ellipsoid, divaricate; pollen yellow to pale yellow, sometimes fading to white and then turning lavender. *Infructescence* with spathe persisting, peduncle 38–44 cm long; berries deep purple, obovoid; seeds 2 per berry.

Anthurium tarapotense is endemic to Peru, where it is apparently confined to premontane moist forest at (300) 360 to 700 m, in the vicinities of Tocache and Tarapoto in Dept. San Martín.

This species is characterized by its obovate to obovate-oblanceolate blades, which are attenuate in the lower third and merge gradually with the petiole, and by the short, D-shaped petioles, frequently more or less intact cataphylls, and tapered or cylindroid, usually maroon or purple spadix.

Two individual live plants, from near Tabalosos, Peru, collected together sterile and bearing the same collection number (*Croat 58130a* and *58130b*), differ substantially and perhaps represent parts of a mixed collection. One of the two, *58130b*, perhaps deserves subspecific recognition. It shares nearly identical leaves with typical *A. tarapotense* (*58130a* representing the species well), but differs in having cataphylls weathering promptly to fibers and a spadix with pistils protruding above the anthers at anthesis and an ellipsoid, caviform stigma bearing stigmatic papillae well below the upper rim. The anthers, immediately after dehiscence (when they are most prominent), are relatively inconspicuous compared to the pistils. In contrast, the pistils of typical *A. tarapotense* are not at all exserted at anthesis and consist of a narrow slit more or less obscured by the anthers. Also, the spadix of *Croat 58130b* is grayish pink, not maroon or yellowish green as in typical *A. tarapotense*.

Anthurium tarapotense is probably most closely related to *A. llewelynii*, which occurs in the same region, but in more exposed sites in tropical dry forest. Both species share similar long-pedunculate inflorescences with moderately short, bluntly tapered spadices and blades markedly arched along the midrib. *Anthurium llewelynii* differs in having larger, narrowly oblanceolate leaves, which end abruptly at the narrowly rounded base, and a reddish olive-green spadix.

PERU. MARISCAL CÁCERES: Dtto. Tocache, Nuevo, Quebrada de Mantención, road to Tocache Progresso, 500–

600 m, *Schunke 13648* (IBE, MO). SAN MARTÍN: hills above Chazute, 200–300 m, 6°34′S, 76°12′W, *Knapp 8349* (MO); Tarapoto, *Ule 5* (B); 360–460 m, *Kennedy 3529* (F); Tarapoto–Yurimaguas, 10.6 km from junction with road to Río Huallaga, 530 m, 06°30′S, 76°21′W, *Croat 58115* (IBE, JBGP, K, MO, NY, USM), *58116* (AAU, MO, P, QCA, SEL, U, UCLA, USM, VDB), *58117* (B, CAS, CM, G, GH, K, LE, M, MO, US, USM, VEN, W, WIS); Río Mayo, Tarapoto–Moyobamba, between Km 562 and 563, 15 km W of Tabalosos, 57 km W of Tarapoto, 600 m, 6°15′S, 76°41′W, *Croat 58130* (CM, IBE, KYO, MO, NY, SEL, USM); Dtto. Tarapoto, Tarapoto–Yurimaguas, near Km 10, 700 m, *Rimachi 5369* (IBE).

Anthurium tenaense Croat, sp. nov. TYPE: Ecuador. Napo: along road between Tena and Puyo, 58.1 km N of Puyo, 600 m, *Croat 49631* (holotype, MO 2738143). Figures 313, 314.

Planta epiphytica; caulis erectus; petiolus 18–19 cm longus, ca. 5–6 mm diam., D-formatus; lamina oblongo-oblanceolata ad oblongo-elliptica, 37–42 cm longa, 9–9.5 cm lata; pedunculus 19.5 cm longus; spatha 8 cm longa, 1 cm lata; spadix (immaturus) 6 cm longus, 3 mm diam.

Epiphytic; stem erect; internodes short, roots numerous, drying whitish; cataphylls unribbed, 6 cm long, drying grayish brown, persisting intact, eventually shredding at base. *Leaves* with petioles (8–9)18–19 cm long, ca. (3–4)5–6 mm diam., ± D-shaped, with obtuse medial rib and with the margins sharply raised adaxially, rounded abaxially; geniculum drying slightly darker and narrower than petiole, (0.4)0.6–0.9 cm long; sheath 2.5–5.5 cm long, free-ending; blades coriaceous, narrowly oblong-elliptic, acute to long attenuate at apex, acute to obtuse (rounded) at base, (23.2)32.5–69 cm long, (5.0–5.6)9–9.5 cm wide, broadest at or above the middle, the margins weakly undulate; both surfaces drying matte, reddish brown, slightly paler below; midrib obtusely angular to broadly convex at base, becoming narrowly acute toward the apex above, more prominently raised below, bluntly acute, becoming narrowly convex toward the apex, darker than surface when dried; primary lateral veins 5–8 per side, departing midrib at 65–90° angle, prominently arcuate to the margin, drying convexly raised and darker than surface above and below; interprimary veins not numerous, less prominent than primary lateral veins; tertiary veins darker than surface when fresh, prominulous; reticulate veins visible on either surface; collective vein arising from near the apex, probably sunken above, raised above and below when dried, 4–10 mm from margin. *Inflorescences* with peduncle (19.5)22.5–60 cm long, (2–3)6–9 mm diam. when dried, ca. (1.5)2.5–3× as long as petiole; spathe green, subcoriaceous, lanceolate with acumen inrolled, (7.6)9–15 cm long, 1–2.5 cm wide, acute at apex, long attenuate at base; spadix green, cylindric to long-tapered, 6–18 cm long, 3–7 mm diam. near base, 1–2 mm diam. near apex; flowers rhombic to 4-lobed, (1–1.5)1.8–2.3 mm long, (0.8–0.9)1.6–1.8 mm wide, the sides moderately straight to jaggedly to smoothly sigmoid; (6–7)8–17 flowers visible in principal spiral, 5 in alternate spiral; tepals minutely granular-papillate, lateral tepals (0.6)0.8–10 mm wide, ± shield-shaped, the inner margins straight to broadly rounded, the outer margins irregularly (2–3)3–4-sided; exposed portion of the pistil rectangular; stigma slitlike, 0.2–0.4 mm long.

Anthurium tenaense is known from Napo Province, Ecuador, near Tena (hence the name), in a tropical wet forest life zone at 400–600 m.

This species is characterized by its thick, more or less elliptic blades, which dry brown, and by its D-shaped petiole, which is rounded abaxially with a broad, obtuse rib, and with raised margins adaxially.

Anthurium tenaense is not easily confused with any other species, although it bears a resemblance to *A. uleanum*, which has thinner leaves mostly drying dark brown, and to *A. harlingianum*, which has broader leaves, more primary lateral veins (12–23) per side, and a slightly to conspicuously curved, salmon-pink to pale violet spadix.

ECUADOR. NAPO: Tena–Puyo, 58.1 km N of Puyo, 600 m, *Croat 49631* (MO); Tena, Estación Biológica Jatun Sacha, 8 km E of Misahuallí, 1°04′S, 77°36′W, 400 m, *Cerón 6073, 6074* (MO).

Anthurium uleanum Engl., Pflanzenr. IV. 23B(Heft 21): 74. 1905.

a. Anthurium uleanum var. **uleanum**. TYPE: Brazil. Amazonas: Rio Juruá Mirim ("Miry"), *Ule 5731* (holotype, B; isotypes, G, MG). Figures 315–317.

Anthurium tenuispadix Engl., Pflanzenr. IV. 23B(Heft 21): 73. 1905. TYPE: Brazil. Amazonas: Rio Juruá Mirim ("Miry"), *Ule 5597* (holotype, B; isotypes, G, MG).

Anthurium tessmannii K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 9:260. 1925. TYPE: Peru. Loreto: Prov. Requena, Cumaria, Río Ucayali, 225 m, *Tessmann 3351* (holotype, B).

Epiphytic; stem to 15 cm long, ca. 2.5 cm diam.; roots dense, green to whitish, smooth to velutinous, 2–5 mm diam.; cataphylls lanceolate, straight to curved, subcoriaceous, 2–11.5 cm long, acute to acuminate at apex, drying reddish brown (B & K

yellow-red 4/10), persisting semi-intact, weathering to reticulate fibers, apex sometimes remaining semi-intact. *Leaves* erect-spreading; petioles (3)10–36 cm long, 2–10 mm diam., D-shaped, sulcate adaxially with medial rib and acute margins, rounded or 2–7-ribbed abaxially; geniculum shaped like petiole, paler and thicker, 0.3–2 cm long; sheath 2.5–6 cm long; blades subcoriaceous, oblong-elliptic to oblong-oblanceolate to obovate, acute to acuminate at apex (the acumen flat), attenuate to acute at base, rarely truncate or subcordate, 20–65 cm long, 5.5–24 cm wide, broadest at or above the middle, the margins broadly undulate; upper surface semiglossy, medium green, drying gray to greenish brown, lower surface matte to semiglossy, slightly paler, drying greenish to gray-green to brown; midrib acutely raised above, acutely to obtusely or convexly raised below; primary lateral veins 5–11 per side, departing midrib at 30–85° angle, straight to arcuate to the margin, acutely raised; tertiary veins prominulous, raised on both surfaces on drying; collective vein arising from near the apex or absent, rarely from below the middle, sunken above, prominulous below, 4–8 mm from margin. *Inflorescences* erect to spreading or spreading-pendent, usually shorter than leaves; peduncle 14–38 cm long, 3–6 mm diam., rarely less on drying, 0.5–3.7(6)× as long as petioles, terete, firm, flexible; spathe spreading to reflexed, rarely erect, subcoriaceous, matte abaxially, medium to pale green, sometimes tinged with red at margins, lanceolate to oblong-lanceolate, 3.5–14 cm long, 0.6–2.7 cm wide, broadest near the base, inserted at 30–50° angle on peduncle, acute to acuminate at apex (the acumen inrolled), acute to obtuse (sometimes decurrent 5–17 mm) at base; stipe 3–7 mm long in front, 2–5 mm long in back; spadix usually pale reddish to purplish (B & K red 8/10), sometimes white to pale green, usually appearing glaucous, cylindroid to slightly tapered, curved, erect, (3)5–15 cm long, 3–5 mm diam. midway, 2–3 mm diam. near apex; flowers rhombic to 4-lobed, scarcely distinguishable, margins obscure, 1.8–2.5 mm long, 1.7–2.5 mm wide, the sides straight to jaggedly sigmoid; 6–10 flowers visible in principal spiral, 6–8 in alternate spiral; tepals matte, weakly papillate, pale olive; lateral tepals (0.5)2–2.2 mm wide, the inner margins broadly rounded to straight, the outer margins 2–3-sided; pistils weakly raised, not emergent, white to pale pinkish; stigma ellipsoid, 0.3 mm long; stamens emerging promptly in a regular sequence from the base, held well above the tepals then retracting to the tepal level, the laterals preceding the alternates by ca. 4–5 spirals, the 3rd stamen preceding the 4th by ca. 2 spirals; anthers white to pinkish, 0.4 mm long, 0.4–0.5 mm wide, inclined over and obscuring the pistil; thecae oblong, divaricate or not; pollen pale yellow, drying white. *Infructescence* ± pendent; spadix to 25 cm long, 1 cm diam.; berries reddish violet, 5 mm long, 2–4 mm diam.; seeds 1–2 per berry, 2.2–2.5 mm long, 0.8–0.9 mm thick, 1.2–1.3 mm wide.

Anthurium uleanum is endemic to the upper Amazon basin, ranging from Ecuador and southern Colombia (Meta, Amazonas, and Vaupés), to Peru (Loreto, Huánuco, Amazonas, and Ucayali), and western Brazil (Acre and Amazonas). It occurs below 550 m in tropical moist, premontane wet, and subtropical wet forest life zones.

This species is distinguished by its long-petiolate, brown-drying leaves, long peduncle, spreading spathe and slender, mostly pale purple, glaucous spadix.

Anthurium uleanum is closest to *A. ernestii*, differing in the presence of a waxy, dustlike bloom on the tepals giving the spadix a matte, pale appearance. A difference that can be used to determine fruiting collections is the slender, often curved, tapered spadix of the present species, rather than a more or less cylindroid, stubby one. *Anthurium uleanum* also has proportionately longer petioles, frequently up to half as long as the blade, and the blades tend to dry brown to dark brown. *Anthurium ernestii* typically has petioles much less than one-third as long as the blade and leaf blades, most often drying greenish with orangish or brownish primary lateral veins. *Anthurium uleanum* has cataphylls which tend to persist intact or semi-intact for a long period before ultimately weathering to fibers. Often there are 2–3 more or less intact cataphylls on a plant. In contrast, the cataphylls of *A. ernestii* persist quite characteristically as an intact network of fine, very pale fibers, and frequently there is little evidence of intact cataphylls on dried specimens.

Another species which may be confused with *A. uleanum* due to having a similar waxy, grayish spadix is *A. manuanum*. See the discussion under that species for distinction from *A. uleanum*.

The new variety of *A. uleanum*, var. *nanayense*, is a morphologically homogeneous taxon restricted to Loreto, Peru, mainly in the Iquitos region. See discussion under the variety for further details.

Synonymized here for the first time is *A. tenuispadix*. Its type (*Ule 5597*), collected at the same locality as that of *A. uleanum*, differs slightly from the latter in having leaf blades attenuate at the

base rather than ending abruptly. Engler separated the two species in his key on presumed differences in the shape of the lateral tepals, but these differences in shape are probably due to their relative ages. Neither the difference in blade shape nor the tepal shape warrants separation of *A. tenuispadix*.

The type of *Anthurium tessmannii* (*Tessmann 3351*), considered here as a synonym, is also toward the larger end of the spectrum in terms of leaf blade size (ca. 65 cm long, 19 cm wide).

Some collections made in the northwestern part of the range of *A. uleanum* in the Province of Napo, Ecuador, differ from Peruvian material and collections from further south in Ecuador in having broader, larger leaf blades with frequently obtuse bases. *Brandbyge & Asanza 30425* and *Pinkley 290* are examples. There is, however, an overall gradation to "typical" Peruvian material within Ecuador.

Several other collections deserve mention. The leaf blades of a collection from the Río Ampiyacu in Loreto, Peru (*Plowman et al. 6541*), are unusual in having only a few, very steeply ascending primary lateral veins (parallel to the margin for most of their length) and a geniculum noticeably shrunken to a narrower diameter than the attending midrib or petiole. The leaf blade, in color and venation, bears some resemblance to that of *A. superbum* subsp. *brentberlinii*. *Harling & Andersson 17571*, *Mexia 6142a*, and *Wurdack 2109* are unusually large plants. The following measurements, contrasted with those of typical material, circumscribe the main differences: petioles 45 cm long (vs. up to 36 cm); leaf blade 85 cm long (vs. up to 65 cm) and up to 31 cm wide (vs. up to 24 cm); peduncle 43–51 cm long (vs. 14–38 cm). The spadix does not differ significantly from that found on those of other plants which are vegetatively more typical and have shorter peduncles.

BRAZIL. ACRE: Cruzeiro do Sul–Rio Branco, 44 km E of Cruzeiro do Sul, Fazenda da Dona Cabuca, 150 m, 7°38′S, 72°35′W, *Croat 62334* (INPA, MO, NY); Rio Moa, Igarape Ipiranga–Aquidaba, Cruzeiro do Sul, *Prance et al. 12049* (INPA, NY, U, US); Cruzeiro do Sul, 150 m, 7°37′S, 72°37′W, *Croat & Rosas 62304* (CM, G, IBE, INPA, K, MBM, MO, NY, QCA, RSA, US); Mpo. Caramari Amazonas, Rio Juruá, N of Cruzeiro do Sul, Lago da Cigana (São Luis), S of Porto Alvaro Nestrinho, 150 m, 7°37′S, 72°36′W, *Croat 62498* (CAS, CM, GB, INPA, K, MO, RSA, SAR, TEX); Mpo. Cruzeiro do Sul, Cruzeiro do Sul–Rio Branco, INCRA headquarters and forest reserve, 160 m, 7°38′S, 72°35′W, *Croat 62629* (INPA, MO). AMAZONAS: Rio Cunhua, basin of Rio Purus, Deni Indian village, 6°43′S, 66°47′W, *Prance et al. 16534* (INPA, NY); Rio Javarí, N of Palmeiras airstrip, 5°08′S, 72°49′W, *Lleras et al. P17101* (INPA); Rio Juruá Mirim ("Miry"), *Ule 5597, 5731* (B, G, MG); Manaus–Porto Velho, 8 km S of Rio Jutai, *Prance et al. 22916* (NY, US). COLOMBIA. AMAZONAS: Río Loretoyacu, vic. Puerto Nariño, *Zarucchi & Schultes 1069* (GH); 100 m, *Schultes 8468* (GH). META: Río Guayabero, 235 m, *Garcia-Barriga & Mejia 17071* (COL); 10 km from Caño Lozada, 350 m, *Pinto et al. 222* (COL, P); VAUPES: Río Apaporis, Río Pacoa, 300 m, 0°20′N, 71°20′W, *Schultes & Cabrera 15221* (COL); Río Pacoa–Río Kananari, 250 m, *Schultes & Cabrera 13703* (COL, US); Soratama, above mouth of Río Kananari, 300 m, 0°5′N, 70°40′W, *Schultes & Cabrera 15164* (US). ECUADOR. NAPO: Parque Nacional Yasuní, 200 m, 0°55′S, 76°11′W, *Cerón & Hurtado 4015* (MO); Pozo petrolero Daimi 2, 200 m, 0°55′S, 76°11′W, *Cerón & Hurtado 4177* (MO); Lago Agrio–Coca, 4.7 km N of Coca, *Croat 50408* (MO); 15 km N of Coca, 450 m, 0°30′S, 76°56′W, *Croat 50412* (AAU, F, GH, K, MO, WIS); San Pablo de Los Secoyas, W–SW of Shushufindi, 300 m, 0°15′S, 76°21′W, *Brandbyge & Asanza 32894* (AAU, MO); Concepción, Hacienda Cotapino, 550 m, 0°48′S, 77°25′W, *Harling et al. 7111* (GB); Coca–El Auca, SE of Francisco de Orellana, road to El Auca, 14.6 km past bridge over Río Napo, 450 m, 0°37′S, 76°40′W, *Croat 50382* (M, MO, NY, QCA, RSA); Lago Agrio, 250 m, 0°6′N, 76°55′W, *Brandbyge & Asanza 30425* (AAU, MO); Lago Agrio–Francisco de Orellana, 26 km N of Coca, 450 m, 0°29′S, 76°55′W, *Croat 50422* (MO, QCA); Lago Agrio–Coca, along Cepe Ferry Rd., 8.8 km S of Río Aguarico on road to Coca (San Francisco de Orellana), *Croat 58519* (MO); Lago Agrio–Puerto El Carmen de Putomayo, 2.2 km SE of Guarumo, 240 m, *Croat 58617* (MO, NY); Tena–Puyo, 61.5 km N of Puyo, 500 m, *Croat 49661* (MO); Río Aguarico, 60 km downstream from San Pablo de Las Secoyas, 220 m, 0°18′S, 76°00′W, *Holm-Nielsen et al. 21120* (AAU); 40 km downstream from San Pablo de Las Secoyas, 230 m, 0°16′S, 76°11′W, *Holm-Nielsen et al. 21095, 21098, 21099* (AAU); Shushufindi, 244 m, *Vickers 220, 254* (F); Dureno, *Pinkley 134, 290* (ECON); 11.4 km W of Lago Agrio, 340 m, 0°8′N, 76°58′W, *Macbryde & Dwyer 1405* (MO); E of Lago Agrio, road to Cepe Ferry Crossing, 450 m, 0°2′N, 76°50′W, *Croat 50426* (MO); Río Cuyabeno, 10 km upstream from Río Aguas Negras, 220 m, 0°10′S, 75°58′W, *Holm-Nielsen et al. 21171* (AAU); Laguna Grande vic., 265 m, *Nielsen 76207* (AAU); Río Napo, Limoncocha, *SEL 78-1155* (cultivated) (MO); Estación Biológica Jatún Sacha, 8 km E of Misahuallí, 450 m, 1°04′S, 77°36′W, *Ceron & Hurtado 3666* (MO); Río Pucino, Lago Agrio, 250 m, *Gentry 9826* (MO); Río Putumayo, Baeza–Puerto El Carmen de Putumayo, 2.1 km W of Guarumo, 43.7 km SE of Lago Agrio, 240 m, 0°07′N, 76°39′W, *Croat 58593* (MO, QCA); Lago Agrio–Río San Miguel, 12.5 km N of Lago Agrio, 0°06′N, 76°50′W, *Croat 50321* (MO); Río San Miguel, 21.2 km N of Lago Agrio, 470 m, 0°8′N, 76°50′W, *Croat 50374* (MO); Yasuní Nacional Parque, 230 m, 0°52′S, 76°05′W, *Cerón 3402* (MO); Río Yasuní, Lago Garza Cocha, 200 m, 1°05′S, 75°47′W, *Lawesson et al. 43345* (AAU); Puerto Napo–Misahuallí, 3.8 km W of Misahuallí, 370 m, 1°02′S, 77°42′W, *Croat 58888* (MO); at junction of Río Tivacuno and Río Tiputini, 220 m, 0°45′S, 76°20′W, *Coello 216* (MO, NY). PASTAZA: Río Curaray, Curaray, 2 km W of the school, 250 m, 1°22′S, 76°58′W, *Holm-Nielsen et al. 21892* (MO); Sucumbios, Reserva Faunistica Guyabeno, S of Laguna Garzacocha, 265 m, 0°01′S, 76°11′W, *Balslev et al. 84679* (AAU); between Laguna Añangueno and Río Cuyabeno, 265 m, 0°01′S, 76°11′W, *Balslev et al. 84882* (AAU);

Río Cuyabeno, Puerto Montúfar, 230 m, 0°06′S, 76°01′W, *Holm-Nielsen et al. 21302* (AAU); Río Namoyacu, 21 km E of Curaray, 200 m, *Harling & Andersson 17569* (GB, MO), *17571* (GB); Río Tiguino, via Auca, 115 km S of Coca, Carretera Petro-Canada, 320 m, 1°15′S, 76°55′W, *Hurtado 1298, 1345, 1548* (MO), *Hurtado & Neill 1506, 1521, 1572, 1573* (MO), *Zak & Rubio 4318B* (MO); Valle de La Muerte, Curaray, 240 m, 1°25′S, 76°52′W, *Holm-Nielsen et al. 22467* (AAU). PERU. AMAZONAS: Prov. Bagua, Río Marañon, Teniente Pinglo, above Pongo de Manseriche, 250–300 m, *Wurdack 2109* (BH, US); Río Santiago, above Pongo de Manseriche, 200 m, *Mexia 6142a* (F, GH, K, UC). HUÁNUCO: Río Pachitea, Puerto Lira, 300 m, *Killip & Smith 26833* (NY, US). LORETO: Iquitos, Amazonas Lodge, *Ellenberg 8463* (MO); Río Corrientes, almost at Ecuadorian border, upriver from Tnte. Lopéz oil camp, 280–300 m, *Gentry et al. 18971* (MO); Río Huallaga, Santa Rosa, below Yurimaguas, 135 m, *Killip & Smith 28769, 28922* (NY, US); Yurimaguas–Balsapuerto, 135–150 m, *Killip & Smith 28285* (NY, S); Río Samaria, Atún Cocha, *Vásquez et al. 4346* (MO); Río Sucasari, tributary of Río Napo, 3°16′S, 72°54′W, *Martin et al. 1747* (ECON, F); Prov. Loreto, San José de Parinari, 150 m, 4°32′S, 74°30′W, *Vásquez & Jaramillo 3354* (MO); Río Corrientes, Valencia, Platanoyacu, ca. 3°10′S, 75°41′W, *McDaniel & Marcos 11131* (MO); Río Macusari, 220–300 m, 2°55′S, 76°15′W, *Lewis et al. 11044* (MO); Prov. Maynas, Ecuador border, 1–5 km from Puerto Peru (military post, 8 km from mouth of Río Gueppi, trib. of Río Putumayo) on trail to Río Napo, 200 m, *Gentry et al. 22038* (F); Iquitos Region, Las Pebas, Río Ampiyacu, 3°10′S, 71°49′W, *Plowman et al. 6541* (GH); Río Yaguasyacu, affluent of Río Ampiyacu, Brillo Nuevo, 2°40′S, 72°00′W, *Plowman et al. 6884* (GH); Río Yavarí, Caserío Paumari, *Revilla 2203* (MO); Prov. Requena, Río Ucayali, Cumaria, 225 m, *Tessman 3351* (B). UCAYALI: Cerro Las Cachoeiras, Quebrada Sapallal, tributary of Q. Shesha, near Peru–Brazil border, 260 m, 8°2′S, 73°55′W, *Gentry & Díaz 58467* (MO); vic. LSV base camp, Quebrada Shesha (trib. of Río Abajao), 65 km NE of Pucallpa, 250 m, 8°02′S, 73°55′W, *Gentry & Díaz 58571* (B, K, MO, US); Prov. Coronel Portillo, Bosque Nacional A. V. Humboldt, 8°40′S, 74°45′W, *Vásquez 3891* (MO).

b. Anthurium uleanum var. **nanayense** Croat, var. nov. TYPE: Peru. Loreto: Mishana, Río Nanay, 120 m, *Solomon 3562* (holotype, MO 2627652). Figure 318.

Differt a var. typicum pro ratione habitu parvioro et seriebus spiralibus ferentibus floribus paucioribus.

Epiphytic, sometimes terrestrial; stem moderately slender, elongate, creeping, up to 100 cm long, 0.7–1.7 cm diam.; leaf scars obscured by root mass, 0.4–1 cm high, 0.9–1 cm wide; roots forming a dense, contiguous mass, ascending or descending, pale green to white, when dried grayish to brownish gray, smooth, fleshy, elongate, tapered, to 10 cm long, (1)2–3 mm diam.; cataphylls subcoriaceous, lanceolate, 3–6 cm long, acuminate at apex, drying brown to reddish brown, persisting semi-intact, eventually deciduous. *Leaves* spreading-pendent to spreading; petioles 5.5–19 cm long, 2–4 mm diam., subterete to C-shaped or sometimes D-shaped, with medial rib and margins raised adaxially, rounded abaxially; geniculum slightly thicker and paler than petiole, sometimes up to 3 cm remote from base of the blade, 0.3–1 cm long; sheath 2–2.5 cm long; blades thinly coriaceous, somewhat chartaceous, broadly elliptic to oblanceolate or broadly oblanceolate, shortly acuminate and apiculate at apex (the acumen downturned, 10–15 mm long), usually attenuate (sometimes acute to obtuse) at base, 22.5–43.5 cm long, 8–17.5 cm wide, broadest at or above the middle, the margins sometimes concave near the base; upper surface matte to semiglossy, medium green, lower surface matte, slightly paler; both surfaces drying matte to sometimes weakly glossy, grayish green to brown, with reddish brown major veins; midrib bluntly to acutely raised at base, becoming narrowly raised toward the apex above, prominently convex to higher than broad and slightly paler than surface below; primary lateral veins 5–7 per side, departing midrib at 40–55° angle, straight then arcuate to the margin, prominently convex above, occasionally raised in shallow valleys, more prominently raised below; interprimary veins if present almost as conspicuous as primary lateral veins, weakly sunken above, raised below; tertiary veins obscure above, flat to slightly raised and somewhat darker than surface below; reticulate veins slightly raised or obscure below when dried; collective vein arising from near the apex or absent, if present weakly sunken to flat above, raised below, drying less prominent than primary lateral veins and raised on both surfaces, ca. 3–7 mm from margin. *Inflorescences* much shorter than leaves; peduncle (4.8)16–28 cm long, drying 1–3 mm diam., 1.2–4.4× as long as petiole, ± terete; spathe spreading, subcoriaceous, green, linear-lanceolate, 4–9.4 cm long, 0.6–1 cm wide, broadest near the base, acuminate at apex (the acumen apiculate, occasionally cuspidate), narrowly acute to almost decurrent at base, the margins meeting at 20° angle; stipe 6–17 mm long in front, 1–2 mm long in back; spadix purplish becoming grayish to white, sometimes reported as green, oblong, weakly tapered, curved, 5–7 cm long, 3–4(5) mm diam. near base, 2–3 mm diam. near apex; flowers ± rhombic, (1.4)1.9–2.1 mm long, (1.1)2.4–2.6 mm wide, the sides smoothly to jaggedly sigmoid; 3–4 flowers visible in principal spiral, 4–6 in alternate spiral; tepals densely and conspicuously papillate to granulose, sometimes appearing glaucous; lateral tepals (1–1.7 mm wide, the inner margins broadly

convex, the outer margins 2–3-sided; pistils slightly raised; stigma broadly ellipsoid, 0.3–0.4 mm long; stamens grouped in a tight cluster above the pistil; anthers 0.4–0.5 mm long, 0.3–0.5 mm wide; thecae oblong, slightly or not at all divaricate. *Infructescence* with spathe persisting, withered; spadix 7.5–9.8 cm long, 0.6–0.9 cm diam.; berries violet, ± ovoid, ca. 3.5 mm long, 3.4 mm diam.; seeds drying yellowish brown, ovoid, darker at the ends, ca. 1.7–2 mm long, 1.2–1.4 mm diam., 1 mm thick.

Anthurium uleanum var. *nanayense* is endemic to Peru in Loreto Department at 100 to 160 m, in the tropical moist forest transitional to tropical wet forest life zone. All collections have been made in the Iquitos region in Maynas Province, many from the Río Nanay (hence the name).

This variety is characterized by its relatively small size, rather elongate stem, broadly oblanceolate to almost obovate leaf blades drying brown and attenuate to narrowly acute at the base and slender, tapered spadix apparently starting as purplish and eventually becoming grayish white (appearing glaucous).

Variety *nanayense* is likely to be confused only with var. *uleanum*, which occurs in the same area and differs in having longer petioles, a longer spadix, more oblong leaf blades, and fewer flowers per spiral. Variety *nanayense* is smaller in overall size than var. *uleanum*, and the uniformity of herbarium specimens of the former is notable.

PERU. LORETO: 17 km SW of Iquitos, *Croat 18460A* (MO); Río Nanay, Iquitos, 100 m, *Plowman 2482* (F, GH); Mishana, 120 m, *Solomon 3559, 3562* (MO); Río Tepiche, Santa Elena, *McDaniel & Marcos 11261* (MO); Prov. Maynas, Iquitos Region, ca. 120 m, *Revilla 3597* (MO), *3685* (AMAZ, F, MO); Río Momón, 130 m, *Croat 19929* (MO), *Díaz & Jaramillo 45* (MO), *Rimachi 7711, 7856, 7858* (IBE, MO); Mishana, 130 m, 3°55′S, 73°35′W, *Vásquez et al. 5319* (MO); Puerto Almendras, 122 m, 3°48′S, 73°25′W, *Vásquez & Jaramillo 3159, 6100, 6618, 7590* (MO); Río Nanay, Casería Mishana, 30 km SW of Iquitos, *Foster 4215, 4227, 4350, 4437* (F); Iquitos–Santa María de Nanay, Mishana, 140 m, 3°50′S, 73°30′W, *Gentry & Emmons 38015* (MO), *Gentry et al. 28905, 31632, 36437* (MO); Santa María de Nanay, 130 m, *Schunke 2453* (F, NY); Río Putomayo, Ecuador border, Guarnición Militar de Gueppi, *Díaz 356* (F); Río Yaguasyacu, affluent of Río Ampiyacu, Brillo Nuevo, 2°40′S, 72°00′W, *Plowman et al. 6854* (GH); Prov. Maynas, Dtto. Iquitos, Iquitos Region, Puerto Almendras, 120 m, 3°48′S, 73°25′W, *Croat 51207* (MO); Iquitos–Puerto Almendras, 15 km from Iquitos, 120 m, 3°47′S, 73°25′W, *Croat 51190* (MO); Río Nanay, Carretera de Picuruyacu, 160 m, *Rimachi 5464* (IBE); Prov. Requena, Río Ucayali, 4°55′S 73°45′W, *Gentry et al. 56361* (MO).

Anthurium upalaense Croat & R. A. Baker, Brenesia 16(Suppl. 1): 97. 1979. TYPE: Costa Rica. Alajuela: between Cañas (Guanacaste) and Upala, near Río Zapote, 1.8–2.7 km S of Rio Canalete, ca. 1,000 m, *Croat 36342* (holotype, MO 2381219; isotypes, CR, F, K). Figures 321, 323, 324.

Epiphytic; stem less than 20 cm long, 1.5–3 cm diam.; leaf scars obscured by root mass and persistent cataphylls; roots moderately dense and numerous, brown to green, scurfy to pubescent, moderately thick and elongate, mostly 2–6 mm diam.; cataphylls lanceolate, coriaceous, acutely 1-ribbed throughout, 11–25 cm long, obtuse to acute to narrowly acuminate at apex, plain green to slightly tinged with red, drying brown, persisting intact, eventually deciduous. *Leaves* erect-spreading to spreading; petioles (6)10–47 cm long, 7–13 mm diam., subquadrangular, broadly sulcate with the margins sharply raised adaxially, 3–5-ribbed abaxially, the surface pale-speckled; geniculum thicker and paler than petiole, sometimes reddish abaxially, 1–2 cm long; blades subcoriaceous to coriaceous, elliptic to narrowly oblong-elliptic to oblong-lanceolate, obtuse to acute to gradually acuminate at apex (the acumen downturned and weakly apiculate), usually acute to narrowly acute (rarely obtuse) at base, (30)40–106 cm long, (4.5)8–34 cm wide, broadest at or near the middle, the margins prominently undulate; upper surface semiglossy, dark green, lower surface semiglossy to glossy, slightly paler; midrib flat to obscurely angular at base, becoming prominently and sharply raised toward the apex and paler than surface above, prominently higher than broad and 3-ribbed at base, becoming prominently and acutely raised toward the apex below; primary lateral veins 10–20 per side, departing midrib at 60–75° angle, almost straight to the collective vein, loop-connected in the upper half, prominently and convexly raised above and below, more so above, paler than surface; interprimary veins less prominent than primary lateral veins; tertiary veins weakly visible, paler than surface above, darker than surface below, flat above and below; reticulate veins partially visible above, darker than surface below, drying prominulous above and below; collective vein arising in the upper half or in the upper third of the blade, flat, when dried slightly raised on both surfaces, 3–5 mm from margin. *Inflorescences* erect to spreading or arching-pendent; peduncle (18)40–54 cm long, 4–10 mm diam., equaling to 1.4–2.4× as long as petiole, light green, weakly pale-speckled, sometimes tinged with purple at base,

terete or 1-ribbed below opening of the spathe, sometimes faintly many-ribbed; spathe erect to reflexed, often rolled up, subcoriaceous, yellow-green, sometimes heavily tinged with violet-purple (B & K yellow-green 6/7.5 to 7/2.5), oblong-lanceolate to lanceolate, (4.5)8–20 cm long, 1–4 cm wide, broadest near the base, inserted at 60–75° angle on peduncle, short-acuminate (the acumen minutely inrolled), acute to decurrent on peduncle at base, the margins meeting at 20–60° angle; spadix green (B & K yellow-green 5/6) to maroon (B & K red-purple 2/7.5), long-tapered, 9–30 cm long, 6–15 mm diam. near base, 4–6 mm diam. near apex; flowers square to rhombic, 2.3–3.4 mm long, 1.7–2.8 mm wide, the sides shallowly sigmoid to straight; 10–20 flowers visible in principal spiral, 7–15 in alternate spiral; tepals matte, inconspicuously pale punctate, with droplets appearing usually after 2 or more anthers emerge; lateral tepals 0.8–1.8 mm wide, the inner margins straight to slightly convex; pistils raised, rectangular to bluntly pyramidal, green to purplish; stigma ellipsoid, green, 0.4–1.1 mm long, brush-like, droplets appearing 12–22 days before stamens emerge, persisting for 5–15 days; stamens emerging ± rapidly from the base or near the base, grouped in a tight cluster above the pistil; filaments retracting, short, ca. 0.2 mm long, 0.5–1 mm wide; anthers pale orange, 0.5–0.6 mm long, 0.7–1 mm wide, contiguous; thecae ellipsoid, scarcely divaricate; pollen orange fading to pale orange to lavender to white or tan. *Infructescence* pendent; spathe reflexed; spadix to 55 cm long, 6 cm diam., with berries emerging ± uniformly throughout; berries red, oblong, acute at apex, tapered to both ends, to 15 mm long; mesocarp mealy, white, sweet; seeds 2 per berry, white, oblong, to 4 mm long.

Anthurium upalaense is known from the Atlantic slope of Nicaragua and Costa Rica, from near sea level to usually less than 700 m (rarely to 1,300 m) in tropical wet forest, premontane wet forest, and wetter parts of tropical moist forest.

This species is distinguished by its persisting, intact cataphylls, moderately long, subquadrangular, sulcate petioles which are 3–5-ribbed abaxially, long-tapered, usually violet-purple spadix and red fruits.

Anthurium upalaense is most closely related to *A. purpureospathum*. See that species for distinguishing characters. It is also apparently related to *A. concolor* from Panama, but differs in having the inflorescence pendent, the spadix long-tapered and more or less green at anthesis, the spathe longer and recurled, and the fresh anthers pale orange.

In Nicaragua *Anthurium upalaense* can be confused with *A. schlechtendalii*, but that species differs in having most cataphylls weathering to fibers, as well as generally shorter, less conspicuously tapered spadix and thicker, more prominently reflexed spathe which is more heavily tinged with purple.

COSTA RICA. Cultivated at Kew: *Brown s.n.* (K), *Bull* 467/1873 (K). ALAJUELA: Florencia–Fortuna, 1 km S of Río Peñas Blancas bridge on road 142, 80 m, 10°22′N, 84°35′W, *Hammel et al. 14054* (MO); NW of New Arenal Volcano, W of Fortuna, *Taylor & Taylor 1170* (NY); San Juan de Lajas, *Smith 1498* (NY); NE of Ciudad Quesada, Artezalea and Methodist Rural Center, *Molina et al. 17264* (EAP, F); Cañas–Upala Road, 3–4 km NNE of Bijagua, along new road to Upala, 400–450 m, 10°45′N, 85°3′W, *Baker & Burger 9859* (CR, F, MO), *Croat 36319* (MO); Río Zapote, 1.8–5 km S of Río Canalete, 100–200 m, *Burger & Baker 9964* (F), *10001* (CR, F, MO), *Croat 36380* (MO), *Croat 36342* (CR, F, K, MO); Lago Arenal, Alto de la Carpintera, Tilarán, *Brenes 18194, 18195* (CR); Río Frío, Los Chiles, 30–40 m, 11°2′N, 84°44′W, *Holm & Iltis 771* (NY), *811* (B, K, P, U). CARTAGO: 24 km NE of Turrialba on road to Limón, 450–525 m, 9°58′N, 83°34′W, *Liesner et al. 15363* (B, MO, WIS); 5 km NE of Río Grande de Orosi at Tapantí, 1,300 m, *Utley & Utley 5062* (MO); Tucurrique, Las Vueltas, *Tonduz 13319* (US); Forests of Tuis, Turrialba, *Pittier 12720* (US); Lake Bonilla, *Pacheco 92* (F). GUANACASTE: El Arenal, *Standley & Valerio 45328* (US); Río Aguacate, Laguna de Arenal, 500 m, *Khan et al. 1085* (BM); Río Chiquito, slope above Lake Arenal, 600–700 m, 10°25′N, 84°46′W, *Haber et al. 4819* (MO). HEREDIA: Puerto Viejo Region, Finca La Selva, *Folsom 9558* (TEX), *Croat 61218* (MO); on Río Puerto Viejo just E of its junction with Río Sarapiquí, 100 m, *Chacón 462* (MO), *Croat 44263, 44297* (MO), *McDowell 389, 1058* (MO); Río Sucio, 20 m, *Croat 35708* (MO); Puerto Viejo–San José, SW of Puerto Viejo, *Burger & Mata 4343* (F, CR). LIMÓN: Cahuita–Limón, vic. Cahuita, 0–10 m, 9°57′N, 83°2′W, *Baker & Burger 17A, 17B* (CR, F, MO); 3 km W and 1.9 km S from Guayacan, highway to Limón, Los Angeles de Siquirres, 1,000 m, *Gomez et al. 20543* (CR, MO, MSC, WIS); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8727* (MO); Pandora, 100 m, *Ocampo 1985* (MO); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8272, 8608* (MO); swamp at Manzanillo de Talamanca, 5 m, 9°38′N, 82°39′W, *Grayum & Burton 4324* (MO); Puerto Viejo de Talamanca–Manzanillo, 10–20 m, 10°38–39′N, 82°40–44′W, *Grayum 3638* (MO); Hone Creek-NW on trail paralleling Río Carbón, *Utley & Utley 660* (F); Limón, *Burger & Burger 8446* (CR, F); Limón–Puerto Viejo, *Baker & Burger 174* (F); hills 3.5 air km S of Islas Buena Vista in Río Colorado, 16 air km SW of Barra del Colorado, 10–120 m, 10°39′N, 83°40′40″W, *Davidse & Herrera 31271* (MO, W); Cerro Coronel, E of Río Zapote, 10–100 m, 10°40′N, 83°40′W, *Stevens 23923* (MO); E of Laguna Danto, 20–170 m, 10°41′N,

83°38′W, *Stevens 23726* (MO); Cordillera de Talamanca, Reserva Biol. Hitoy Cerere, Cerro Bitarkara, 800 m, 09°38′25″N, 83°08′15″W, *Herrera & Solís 2493* (CR, MO); Tsaki, *Pittier 9509* (BR), *Tonduz 9507* (BR, CR); Parque Tortuguero, 4 m, 10°31′N, 83°30′W, *Robles 1331* (F, L, MO), *1332* (MO); Forests of Shirores, Talamanca, *Tonduz 9228* (BR); Quebrada Mata de Limón headwaters, Finca Anai, Sixaola, 25–40 m, 9°35′N, 82°39′W, *Grayum 4501* (MO); Río Catarata, Bribri, 50 m, *Croat 43221* (F, K, MBM, MO, NY, RSA, SEL); Río Madre, 11 mi SW of Limón, Hwy. 32, 10 m, *Croat 43305* (AAU, CR, G, GH, K, LE, MO, NY, P, RSA, UCLA, W, WIS); Río Reventazón, Cairo, Hamburg Finca, *Standley & Valerio 48869* (US). PUNTARENAS: Cantón of Coto Brus, Las Cruces Tropical Botanical Garden, 6 km W of San Vito de Java, 1,200 m, *Croat 57257* (CR, MO). NICARAGUA. CHONTALES: 4 km NW of Santo Domingo, 250 m, 12°18′N, 85°7′W, *Grijalva & Soza 3749* (MO); N of Cuapa, 700 m, *Atwood & Neill AN35* (MO); confluence of Río El Jordan and Río La Pradera, Hacienda San Martín, 390 m, 12°17′N, 85°15′W, *Stevens 21826* (MO); Cerro Oluma, NE side, above Hacienda San Pedro Oluma, 600–700 m, 12°18′N, 85°23′W, *Nee 28359* (MO). JINOTEGA: Río Coco, Rapido Plis, 200 m, 14°0–10′N, 85°20–30′W, *Stevens et al. 16823* (MO). MATAGALPA: above Matagalpa–Siuna road, La Gloria, 78 km from Matagalpa, 600 m, 13°15′N, 85°35′W, *Moreno 17218* (MO); Cerro Musun, Río Bilampi, 500–800 m, *Neill 1782* (MO); Wanawas, 200–500 m, *Araquistain & Moreno 2739* (BM, LE, MBM, MO), *2744* (MO); 4 km SW of Wanawas, 200–500 m, 13°0–1′N, 85°14′W, *Araquistain & Moreno 2658* (MO, NY); Quebrada Las Carpas, El Limón, 580 m, 13°15′N, 85°34′W, *Stevens & Moreno 19715* (MO). RÍO SAN JUAN: Río Santa Cruz–Caño Santa Crucita, La Palma, 40–60 m, 11°2–4′N, 84°24–26′W, *Stevens 23437* (MO), *Neill 1552* (MO); 1 km W of San Juan del Norte, 0–2 m, 10°55′N, 83°43′W, *Rivière 222* (MO); Río San Juan, San Juan del Norte, Caño la Barca, 0–10 m, *Araquistain 3283, 3302, 3401* (MO), *Martinez & Rivière 1952* (MEXU), *1957* (MEXU, MO). ZELAYA: Waslaya–Siuna, 6 km W of La Cuesta El Balsamo, Rosa Grande, 260–300 m, 13°38′N, 85°2′W, *Moreno 19190* (MO); Río Blanco–Río Copalar, 29–31 km E of Río Blanco, 200–400 m, 12°50–55′N, 85°0–5′W, *Stevens 12143, 12182, 12206* (MO); El Recreo, *Atwood & Neill AN233* (MO); stream 1 km N of Las Mercedes, 160–180 m, *Vincelli 328A* (MO); Monkey Point, 3 km above Caño El Pato, 10 m, 11°35′N, 83°42′W, *Moreno 12466* (MO); Siuna–Matagalpa, 31.4 km beyond Río Uli, 8.9 km beyond Rosa Grande La Balsamo, 200 m, *Stevens 7524* (MO); Caño Monte Cristo, La Grupera, 10 m, 11°33′N, 84°48′W, *Moreno & Sandino 14688, 14655* (MO); village of Germán Pomares, Las Benitas, 100 m, 11°36′N, 83°51′W, *Moreno & Sandino 14933* (MO); Cerro Waylawas (Peñas Blancas), 5 k S of Wany, 13°30′20″N, 84°45′25″W, *Grijalva & Burgos 1685* (MO); Río Punta Gorda, Atlanta, 10 m, 11°34′N, 84°1′W, *Moreno & Sandino 12755* (MO); Río Sucio, 0.5 km E of 1st suspension bridge E of Bonanza, 140 m, 14°1′N, 84°34′W, *Stevens 12317* (MO).

Anthurium validifolium K. Krause, Notizbl. Bot. Gart. Berlin-Dahlem 11: 607. 1932. TYPE: Panama. Chiriquí: forests along Río Ladrillo, above El Boquete, 1,200–1,300 m, *Pittier 3052* (holotype, US). Figures 322, 325–327, 231, 232.

Epiphytic; stem to 16 cm long; leaf scars 2.5 cm wide; roots numerous, descending, green, smooth, 5–15 mm diam.; cataphylls moderately coriaceous, 20–30 cm long, long-acuminate at apex, medium green, sparsely pale-speckled, matte, drying tan (B & K yellow-red 9/10), persisting ± intact. *Leaves* erect-spreading; petioles 20–27 cm long, 7–10 mm diam., quadrangular to bluntly D-shaped, flattened to broadly and shallowly sulcate adaxially, rounded abaxially, surface pale-speckled; geniculum thicker and slightly paler than petiole, becoming fissured transversely with age, 3–4.5 cm long; blades coriaceous, oblong to oblong-oblanceolate or lanceolate, acute at apex (the acumen apiculate), acute and decurrent to rounded at base, 47–69 cm long, 10–19 cm wide, broadest at or near the middle, the margins broadly undulate; both surfaces matte, dark green above, paler below; midrib flat at base, becoming obtusely angular and narrowly raised at apex above, bluntly 2-ribbed and higher than broad at base, becoming prominently and convexly raised toward the apex below; primary lateral veins numerous, departing midrib at 60–70° angle, ± straight, arcuate near the margin, sunken in grooves above, raised below, paler than surfaces; interprimary veins obscure above, darker than surface below; tertiary veins obscure above, darker than surface below; collective vein arising in the upper third of the blade, weakly sunken above, raised below, less prominent than primary lateral veins, 5–6 mm from margin. *Inflorescences* spreading, shorter than leaves; peduncle 33–39 cm long, 9–12 mm diam., 2× as long as petiole, subterete; spathe reflexed, coriaceous, dark green (B & K yellow-green 5/10), ovate-lanceolate, 16–17 cm long, ca. 4 cm wide, inserted at 45° angle on peduncle, acuminate at apex, rounded at base; stipe 7–13 mm long in front, ca. 3 mm long in back; spadix pale lavender to violet-purple (B & K purple 6/5 to 5/2.5), tapered, 15–23 cm long, (4)6–12 mm diam. near base, 2–5 mm diam. near apex; flowers rhombic, 3–3.5 mm long, 3.1–3.6 mm wide, the sides straight to weakly sigmoid; 7–8 flowers visible in principal spiral, 8–10 in alternate spiral; tepals matte; lateral tepals 1.5–1.8 mm wide, the inner margins broadly convex; pistils scarcely emergent, green; stigma ellipsoid, ca. 0.6 mm long, droplets appearing for ca. 1 week before stamens emerge; stamens emerging rapidly from near the base or sometimes from

near the middle, lateral stamens emerging to midway before alternates appear; anthers yellow-orange, ca. 1 mm long, 1.2 mm wide, inclined over the pistil; thecae oblong-ellipsoid, scarcely divaricate; pollen yellow-orange (B & K yellow-red 8/5). *Infructescence* pendent; spathe twisted; spadix 24–26 cm long, 2.3–2.5 cm diam.; berries bright orange, obovoid, flattened at apex, 0.8–15 mm long; pericarp thin, ± transparent; mesocarp fleshy, orange, with minute raphide cells; seeds 1–2 per berry, pale yellow, ovoid, with a somewhat flattened appendage at both ends, enveloped by somewhat dry, sac-like structure.

Anthurium validifolium is known from Chiriquí Province in Panama and adjacent Puntarenas Province in Costa Rica. Most collections have been made in lower montane rain forest, from 1,200 to 2,300 m.

This species is characterized by its large, moderately thick, lanceolate leaf blades, lavender to purple spadix, and bright orange, obovoid berries.

Anthurium validifolium is probably most closely related to *A. seibertii* and *A. protensum*, which share a similar inflorescence and orange berries. It differs from both in having broader and thicker leaf blades. Its subquadrangular petiole is somewhat intermediate between the terete petiole of *A. protensum* and the sharply quadrangular petiole of *A. seibertii*. Although this suggests *A. validifolium* may be a hybrid between *A. protensum* and *A. seibertii*, its thicker, proportionately shorter blades are not a feature of those species.

The specimen from Puntarenas was cultivated at Las Cruces Tropical Botanical Garden, but was reported to have been collected locally by Robert Wilson, founder of the garden.

COSTA RICA. PUNTARENAS: Cantón of Coto Brus, Las Cruces Tropical Botanical Garden, 6 km W of San Vito de Java, *Croat 44445, 57258, 57279* (MO). PANAMA. CHIRIQUÍ: 2 mi. N of El Hato del Volcán, *Croat 10667* (B, F, GH, K, MO, NY, PMA, RSA, US); Cerro Pelota, 2,300 m, 8°54′N, 82°43′W, *Knapp 1513* (F, MO); Cerro Pelota, lower slopes, 1,800–2,000 m, 8°53′N, 82°43′W, *Knapp 1497* (K, MO); ridge S of Cerro Pelota, 1,700–2,200 m, 8°53′N, 82°43′W, *Knapp 1522, 1523, 1526, 1528, 1529* (MO); Cerro Punta, 4.7 mi. E of Volcán, 1,600 m, 8°49′N, 82°38′W, *Croat 66204* (MO); Volcán–Río Sereno, 1,520 m, *Croat 66321* (MO); Bambito–Cerro Punta, *Croat 10553* (MO); *Croat 10554* (F, MO); Boquete Region, 9 km WNW of Boquete, 1,870 m, *Davidse & D'Arcy 10309* (MO, PMA); Cerro Pando, NW side, *Croat 15971* (MO, NY); Río Colorado, 1,200–1,400 m, 8°50′N, 82°43′W, *Hamilton & Stockwell 3532* (MO); Río Ladrillo, El Boquete, 1,200–1,300 m, *Pittier 3052* (US).

Anthurium vaupesianum Croat, sp. nov. TYPE: Colombia. Vaupés: vic. Mitú, 2–3 km below Urania, Río Vaupés, *Zarucchi & McElroy 1172* (holotype, GH; isotype, COL). Figures 329, 330.

Planta epiphytica; internodia brevia, 1–2 cm diam.; cataphyllum lanceolatum; petiolus 4–9 cm longus, 3–5 mm diam., complanatus et obtuse costatus adaxile, abaxile rotundatus ad trinervis; lamina coriacea–subcoriacea, oblanceolata-obovata, abrupte attenuate in dimidio inferiore, 20–62 cm longa, 9–26 cm lata; nervis primariis lateralibus 6–12 utroque; pedunculus (16)36–70 cm longus; spatha oblonga-linearis, viridis-olivacea, 9–20 cm longa, 0.6–1.5 cm lata; spadix brunneo-rubellus aut virellus, sessilis vel stipitatus, ad 3.5 cm, longe contractus, 20–35 cm longus, 3–4 mm diam.; baccae violaceae.

Epiphytic; stem to 9 cm long, 1–2 cm diam.; roots dense, ascending, fuzzy, soon glabrous, 3–4 mm diam.; cataphylls subcoriaceous, lanceolate, 3–5 cm long, acuminate at apex, drying dark reddish brown, semi-intact, persisting briefly. *Leaves* erect-spreading; petioles 4–9 cm long, 3–7 mm diam., D-shaped, flattened and conspicuously and obtusely ribbed adaxially, rounded to weakly angulate or weakly 3-ribbed abaxially; geniculum thicker than petiole, 0.5–1 cm long; sheath 3–7 cm long; blades coriaceous to subcoriaceous, oblanceolate-obovate, acute at apex, narrowly attenuate, ending narrowly acute to obtuse at base, 20–62 cm long, 9–26 cm wide, broadest above the middle, the margins usually flat, sometimes weakly and broadly undulate; upper surface semiglossy, medium green, lower surface weakly glossy, paler; both surfaces drying grayish to grayish brown; midrib convexly raised at base, becoming sharply raised (knifelike) toward the apex above, acutely raised at base, becoming convex toward the apex below; primary lateral veins 6–12 per side, departing midrib at 30–50° angle, straight to arcuate-ascending to the margin, raised in shallow grooves above; tertiary veins conspicuously sunken above, conspicuously raised below; collective vein arising from near the apex or absent, sunken above, raised below, 6–12 mm from margin. *Inflorescences* erect to pendent, ± equaling leaves; peduncle (16)36–70 cm long, (1)3–4 mm diam., (2.7)4–7.7× as long as petiole, terete; spathe spreading to reflexed, subcoriaceous, green to brownish green, sometimes mottled purple, oblong-linear, 9–20 cm long, 0.6–1.5 cm wide, inserted at 40° angle on peduncle, acute at apex, attenuate at base; spadix brown to reddish to greenish or gray-brown (once reported as white), long-tapered, sessile or stipitate to 3.5 cm, somewhat curved, 20–38 cm long, drying 3–4 mm diam.

midway, 2 mm diam. near apex; flowers rhombic, 1.4–1.8 mm long, 1.2–1.4 mm wide, the sides straight to smoothly or jaggedly sigmoid; 3–5 flowers visible in principal spiral, 3 in alternate spiral; tepals semiglossy, minutely papillate; lateral tepals 0.7–0.9 mm wide, the inner margins straight to rounded, the outer margins 2-sided; anthers 0.4 mm in both directions, inclined over and obscuring the pistil; thecae ellipsoid, slightly divaricate. *Infructescence* with spathe persisting ± intact; spadix 0.9 cm diam.; berries violet.

Anthurium vaupesianum is endemic to southern Colombia in Vaupés (hence the name) and Amazonas departments, where it is an epiphyte at 130–250 m in tropical premontane wet forest.

This species is characterized by its small size, short petioles, obovate-oblanceolate leaf blades drying grayish-brown and usually rather abruptly attenuate in the lower half with conspicuously concave margins, and by its very slender, long-tapered spadix. It is probably most closely allied to *A. anorianum* from Antioquia Dept. in northern Colombia. Although it has a similar long, slender spadix, the latter has larger leaves that have convex margins in the lower half and are obtuse to acute at the base, and peduncles that dry reddish. It occurs at 300 to 750 m, in a region separated from *A. vaupesianum* by two major mountain ranges.

COLOMBIA. AMAZONAS: Río Caqueta, La Padrera, 240 m, *García-Barriga 14605* (COL). AMAZONAS-VAUPÉS: Río Apaporis, Río Pacoa–Río Cananarí, Soratama, 250 m, *Schultes & Cabrera 13535, 13796* (ECON), *12772, 13621* (US); Jinogoje, mouth of Río Piraparana, 230 m, 0°15′S, 70°30′W, *Schultes & Cabrera 19820* (US). VAUPÉS: 2 km SE of Mitú, 200 m, 1°14′N, 70°14′W, *Croat 56795* (AAU, COL, F, JAUM, K, M, MO, NY, RSA, US); Río Kubiyu, vicinity of Mitú, *Zarucchi & Davis 1185* (COL, GH); Río Piraparana, middle course, *Schultes & Cabrera 17128* (US); Río Vaupés, Mitú, 2–3 km below Urania, *Zarucchi & McElroy 1172* (COL, GH).

Anthurium venosum Griseb., Cat. Pl. Cub. 219. 1866. TYPE: Cuba. Westindische Province, *Wright 3209* (holotype, MO 2058854; isotypes, NY, US). Figures 328, 349, 350.

Terrestrial or epilithic. Stem short, ca. 1.5–2 cm diam.; roots dense, grayish, moderately to densely velutinous, moderately elongate, ca. 3–5 mm diam.; cataphylls subcoriaceous, lanceolate, 3–6 cm long, acute at apex, brown (B & K yellow 4/2.5), persisting semi-intact, eventually as a reticulum of fibers. *Leaves* with petioles (5)15–40 cm long, ca. (3)6–10 mm diam., terete to weakly sulcate, medium green; geniculum 1 cm long; blades coriaceous to subcoriaceous, oblong-ovate, acute to shortly acuminate at apex (the acumen shortly apiculate), ± rounded to subcordate or weakly cordate at base, (17)24.5–46 cm long, (12.5)15.7–21.5 cm wide, broadest at or near the middle, the margins broadly undulate; anterior lobe (15)22.5–40 cm long; the posterior lobes (3.5)5–6 cm long, (4)5–6 cm wide, directed downward and rounded at apex; sinus mostly triangular, rarely arcuate with the blade decurrent on petiole to shallowly triangular, 1–3 cm deep; both surfaces glossy, moderately bicolorous, drying yellowish brown to yellowish green; midrib convexly raised above, paler than surface, more prominently raised below; basal veins 3–4 pairs, all free to base, raised above and below; primary lateral veins 5–9 per side, departing midrib at 40–65° angle, straight to broadly arcuate, prominently raised and paler than surface above and below; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins prominulous; reticulate veins raised; collective vein arising from near the apex or absent. *Inflorescences* spreading; peduncle 12–84 cm long, ca. 3–8 mm diam., 1.4–2.9× as long as petiole; spathe reflexed, subcoriaceous, green, lanceolate to linear-lanceolate, 3–10 cm long, 1–1.5 cm wide, broadest near the base, acuminate at apex (the acumen sometimes cuspidate, 6–7 mm long), acute to decurrent at base; stipe 15–17 mm long in front, 5 mm long in back; spadix brownish green to purplish brown, tapered, ± erect to curved, 2–15 cm long, 5–6 mm diam. near base, 2–3 mm diam. near apex; flowers rhombic, 2.5–2.9 mm long, 1.4–2 mm wide, the sides straight to smoothly sigmoid; 5–6 flowers visible in principal spiral, 8–9 in alternate spiral; tepals weakly roughened; lateral tepals 1.3–1.7 mm wide, the inner margins broadly convex, the outer margins 2-sided; pistils pale green; stigma ± ellipsoid, 0.3–0.4 mm long; anthers 0.3–0.4 mm long, 0.5–0.7 mm wide; thecae ± ovoid, not at all or only slightly divaricate. *Infructescence* with spathe persisting; spadix to 17 cm long, to 2 cm diam.; berries orange-red, ± ovoid to obovoid, 6–6.5 mm long, 4.5–6.2 mm diam.; seeds 1–2 per berry, brown with numerous pale raphide cells on the surface, 3.7–4 mm long, 1.7–2.8 mm diam., 1.2–1.8 mm thick.

Anthurium venosum is known only from Cuba and is apparently restricted to Piñar del Río Prov-

ince, especially around Viñales, where it occurs on limestone cliffs at less than 300 m.

This species is distinguished at once by its rather small, oblong-ovate leaf blades with conspicuous basal veins (3 to 4 pairs) and more or less rounded to shallowly cordate leaf bases, and brownish green, tapered spadix.

Anthurium venosum is a distinctive species within the section, but has been confused with other species in the West Indies. Most notable perhaps is a population of plants on Jamaica in St. James Parish at 700 m, which resembles both *A. mancuniense* C. D. Adams and the present species. This was reported by Adams (1972) for Jamaica based upon *Proctor 7977* and *Proctor & Stern 11748*. Although these specimens look more like *A. venosum*, a re-collection (*Croat 69757*) proves that it belongs to neither species and probably represents a new species not belonging to sect. *Pachyneurium*.

CUBA. NO FURTHER LOCALITY: *Wright 3209* (MO, NY, US); Cultivated at Havana Botanical Garden, *Croat 69756* (MO). PINAR DEL RÍO: 250 m, *Rutten-Pekelharing & Gillavry 425* (B), *Hermann 3183* (NY, US); Mogote de la Baudera Viñales, *Leon 14378* (NY); Mogote de La Jagua, La Jagua, Consolación del Norte, *Roig & Asary 2540* (NY); San Vicente, Viñales, *Leon 22746* (US); Sumidero, *Shafer 13378* (A, BM, NY, US); Baños San Vicente, *Britton et al. 7314* (NY, US); Viñales, *Killip 13583* (US); Viñales, Mogote de Santo Tomás, *Arias s.n.* (MO); Sierra de Viñales, *Ekman 16539b* (NY, US).

Anthurium vinillense Bunting, Phytologia 64: 462–463. 1988. TYPE: Venezuela. Amazonas: Dept. Río Negro: hilly savanna, Serranía de Vinilla, ca 20 km SW of Mavaca, 2°26′N, 65°20′W, ca. 420 m, *Huber 6201* (holotype, VEN, isotypes, MO, NY). Figure 354.

Description based on dried material only. Usually terrestrial, sometimes epilithic, to ca. 35 cm tall; internodes short; cataphylls narrowly triangular, 5.5 cm long, narrowly acute at apex, drying reddish brown, the uppermost persisting semi-intact, promptly weathering to fibers. *Leaves* erect; petioles 3.2–5.2 cm long, less than 5 mm diam., C-shaped, weakly sulcate with raised margins and an obscure medial rib adaxially, rounded abaxially; sheathing to midway; 5.6–7.3× as long as petiole; geniculum scarcely thicker and drying darker than petiole, ca. 0.5 cm long; blades coriaceous, elliptic to obovate-elliptic, acuminate at apex (the acumen short, with margins thickened and turned upward), acute to obtuse at base, 16–28 cm long, 4.3–9.5 cm wide, broadest at or slightly above the middle, 3–3.6× longer than broad; upper surface inconspicuously punctate, lower surface densely dark glandular-punctate (those glands ca. 1.5 mm diam.); both surfaces drying yellow-green, glossy; midrib convexly raised on both surfaces; primary lateral veins 5–8 per side, departing midrib usually at ca. 10° angle from midrib, then spreading at 40° angle, moderately straight or weakly to markedly arcuate to the margin; collective vein lacking or arising from second to last primary lateral vein. *Inflorescences* erect, longer than leaves; peduncle 27–39 cm long, 5.6–7.3× as long as petiole; spathe twisted, green, linear-lanceolate, to 6 cm long, 1 cm wide, thickened at base, inserted at 30° angle on peduncle, acuminate at apex (the acumen inrolled), decurrent for 7–10 mm at base, promptly drying and ultimately deciduous or nearly so; prominently and closely veined adaxially, densely purple-punctate adaxially (on surface and veins) with pale, short raphide cells; stipe 4–6 mm long; spadix green tinged with maroon, scarcely tapered at apex, erect, to 10.5 cm long, 5–6 mm diam.; flowers rhombic, 2–2.3 mm long, 1.6–1.9 mm wide, the sides moderately straight; 7–9 flowers visible in principal spiral; tepals obscurely pale-punctate; lateral tepals 1.6–1.9 mm wide, the inner margins broadly rounded, the outer margins 2-sided; pistils not at all exserted; stigma linear, 0.6 mm long; stamens held just above tepals in a tight cluster, inclined over and obscuring the pistil; anthers 0.4 mm long, 0.7 mm wide; thecae ovoid, moderately divaricate. *Infructescence* with spathe withered, bearing berries in the basal fourth only; berries dark wine-red toward apex, paler to whitish in lower part, to 7 mm diam.; seeds 2 per berry, slightly flattened, 3.8 mm long, 2.6 mm diam.

Anthurium vinillense is endemic to Venezuela, known only from the type locality in the Serranía del Vinilla in southern Amazonas.

This species is characterized by its small size, short petioles that are sheathed to half their length, glandular-punctate, elliptic to subelliptic, coriaceous blades which dry with prominently raised reticulate veins on both surfaces, and dark wine-red berries.

Anthurium vinillense is closely related to both *A. xanthoneurum* and *A. bonplandii* subsp. *guayanum* and will perhaps prove to be only a subspecies of *A. bonplandii*. The type locality of *Anthurium vinillense* is a relatively remote and poorly explored area. *Anthurium bonplandii* subsp. *guayanum* has been collected in numerous localities to the north and south of the Serranía del Vinilla, but plants of subsp. *guayanum* are much

larger and never have the reticulate veins prominently raised.

VENEZUELA. AMAZONAS: Dpt. Río Negro, ca. 20 km SW of Mavaca, 420 m, 2°26′N, 65°20′W, *Huber 6201* (MO, NY, VEN).

Anthurium wagenerianum K. Koch & Bouché, Ind. Sem. Hort. Berol. App. 7. 1853. TYPE: Venezuela. Caracas, *Wagener s.n.* (Type destroyed; cultivated at Vienna; Schott illustrations 542–544 serve as lectotype). Figures 335–338.

Anthurium huequeense Bunting, Phytologia 60(5): 295. 1986. TYPE: Venezuela. Cultivated at Jard. Bot. Maracaibo, originally collected by van der Werff in Falcón: Dtto. Zamora, delta of Rio Hueque, Coro–Morón Hwy., 100 km E of Coro, *Bunting 7704* (holotype, NY, isotypes, MO, VEN).

Terrestrial, often epilithic; stem short, 1.5–3.5 cm diam.; roots moderately numerous, ascending to descending, greenish gray, often fuzzy or woolly-pubescent, thick, blunt, to 15 cm long, 2–7 mm diam.; cataphylls subcoriaceous, broadly lanceolate, 3–7 cm long, acute at apex, yellowish green weakly tinged with red, drying brown to reddish brown, usually with visible raphide cells, persisting semi-intact, eventually as coarse linear fibers. *Leaves* erect to erect-spreading; petioles (4)6–25 cm long, drying (1)4–10 mm diam., subquadrangular to trapezoidal or D-shaped, flattened to broadly sulcate to obtusely V-sulcate adaxially, with the margins sharply to bluntly raised, rounded to 3-ribbed abaxially; geniculum paler and thicker than petiole, becoming fissured transversely with age, 0.5–1.5 cm long; blades subcoriaceous to coriaceous, narrowly to broadly elliptic or oblanceolate, acute to obtuse or rounded at apex (the acumen briefly cuspidate), acute to attenuate at base, (8)17–70 cm long, (4)6–30 cm wide, broadest at or above the middle, the margins conspicuously wavy, minutely undulate when dried; both surfaces matte to weakly glossy to semiglossy, dark to medium green above, slightly paler below, with linear raphide cells conspicuous on drying (especially below), occasionally with pustules on either surface; midrib flat to weakly angular at base, becoming narrowly acutely raised toward the apex above, prominently 3-ribbed to convexly raised at base, becoming convexly raised toward the apex below; primary lateral veins (3)4–7 per side, departing midrib at 30–65° angle, ± straight then arcuate close to margin, prominently and narrowly convex above, less narrow and prominent below; interprimary veins few, especially in juvenile leaves, obscure; tertiary veins sunken to obscure above, weakly raised and darker than surface below; collective vein arising from near the apex, weakly sunken above, somwhat raised and darker than surface below, 2–10 mm from margin. *Inflorescences* erect to spreading, shorter than leaves; peduncle 8–54 cm long, 4–6 mm diam., (1)1.5–3× as long as petiole, medium green tinged reddish at base, terete; spathe spreading to reflexed, subcoriaceous to moderately coriaceous, plain green to tinged with red-purple, lanceolate to broadly lanceolate, sometimes ovate, 2–6 cm long, 0.5–2 cm wide, broadest at or near the middle, inserted at 80–90° angle on peduncle, acute to acuminate at apex (the acumen inrolled, 2–5 mm long), obtuse to decurrent at base; spadix creamy to green to gray-green at anthesis, becoming red to purple-violet post-anthesis, cylindroid to weakly tapered, sessile or stipitate 1–25 mm, mostly erect, sometimes slightly curved, held at 130–180° angle from peduncle, (1.5)4–12.5 cm long, 5–12 mm diam. midway; flowers mostly square to occasionally 4-lobed, (1.2)1.6–3.1 mm in both directions, the sides straight to smoothly sigmoid; 5–10 flowers visible in principal spiral, 5–8 in alternate spiral; tepals matte, very minutely papillate, with pale protuberances when dried; lateral tepals 0.8–1.8 mm wide, the inner margins straight to convex, often broadly so, the outer margins 2-, occasionally 3-sided; pistils early-emergent, semiglossy, densely and minutely papillate, bright green; stigma linear to ellipsoid, 0.2–0.3 mm long; stamens emerging from the base, the laterals preceding the alternates by 6–13 spirals, the 3rd preceding the 4th by 3–6 spirals, held above the tepals in a circle around the pistil; filaments not exserted when dried; anthers creamy, sometimes tinged with pink, 0.6–0.9 mm long, 0.6–1 mm wide; thecae oblong-ellipsoid, not at all or only slightly divaricate; pollen faintly spicy scented, pale yellow to creamy white fading to white. *Infructescence* spreading to pendent; spathe persisting, green; spadix to 13 cm long, to 2 cm diam., with berries scattered throughout; berries red to purple, oblong to obovoid, acute to mammilliform at apex, 6–8.2 mm long, 3.2–4.5 mm diam.; pericarp thickened, with numerous raphide cells; seeds 2 per berry, broadly ellipsoid or oblong-ellipsoid, 3.2–5 mm long, 1.6–3 mm diam., 0.8–1.6 mm thick, attached to carpel wall at radicle end by a thick strand of fibers running midway down the carpel to the basal end of the fruit.

Anthurium wagenerianum is known from the Cordillera Costal in Venezuela and from Curaçao

in the Netherlands Antilles. It is found on steep, rocky cliffs and dry slopes, rarely reported from primary forest, from sea level to 600 m in tropical moist, tropical dry, and premontane dry forest life zones.

This species can be distinguished by the blades, which dry with pale raphide cells conspicuously visible under low magnification and with conspicuous undulations along the margin, and by the petiole, which is more or less quadrangular, adaxially flat to broadly sulcate, and abaxially usually squared or 3-ribbed. The spathe and spadix of *A. wagenerianum* are both quite small, and the spadix is cream-colored to green at anthesis, sometimes with the tepals fainty tinged with purple.

Anthurium wagenerianum is deceptively similar to *A. crassinervium* in habit, range, and leaf shape. The above-mentioned blade and petiole characteristics, however, aid in identification of dried specimens. Furthermore, dried abaxial leaf surfaces of *A. wagenerianum* do not demonstrate the highly light-reflective character nor the readily distinguished concentric epidermal cell pattern of *A. crassinervium* (see that species for more details). The spathe and spadix of *A. wagenerianum* are, moreover, quite short and stout in comparison with those of *A. crassinervium*. Both species have red berries basally attached to the spadix by tepalar fibers at maturity. *Anthurium wagenerianum*, however, has a drier berry upon rehydration, its seeds being attached to the inner carpel wall at its apical end by a thick strand of fibers running midway down the carpel toward the basal end of the fruit, as in *A. bonplandii*. *Anthurium crassinervium*, in contrast, has seeds attached to the rehydrated berry by a mucilaginous substance typically found in fruits of most members of sect. *Pachyneurium*. Another feature separating *A. wagenerianum* from *A. crassinervium* are the pistils which are earlier emergent at anthesis in *A. wagenerianum* than is true of *A. crassinervium*.

Bunting et al. 11993 is included in *A. wagenerianum* with reservation. It is reportedly an epiphyte from a wet forest life zone, with an adaxially convex petiole. All three of these characteristics conflict with the norm for *A. wagenerianum*. Its lower leaf epidermal characteristics, stubby spadix, and short spathe suggest that its placement in this species is, however, correct.

Anthurium huequeense was compared by Bunting (1986) with *A. crassinervium*, but is in fact conspecific with *A. wagenerianum* and cannot be distinguished from typical material of the latter.

NETHERLANDS ANTILLES. CURAÇAO: Christoffel Mountain, *Tuinen 79GR00095* (K). VENEZUELA. CARABOBO: Puerto Cabello, 100 m, *Curran & Haman 1140* (GH, US); Las Trincheras–El Cambúr, 1.5 km N of bridge over Río Trincheras, N edge of Las Trincheras, 0–500 m, 10°21′N, 68°05′W, *Croat 54543* (CAS, F, MO, RSA, SEL, US), *54544* (GH, K, MO, NY); Puerto Cabello–Valencia, El Cambúr, *Bunting 2848, 2854* (NY); 100–300 m, *Bunting 13512* (cultivated at MO). DISTRITO FEDERAL: W of Naiguatá, 0 m, *Gentry & Berry 14735* (MO); Río Las Caracas, above town of Las Caracas, 100 m, *Croat 21620* (MO). FALCÓN: Sierra de San Luis, Piedra de Agua, 600 m, 11°08′N, 69°40′W, *Liesner et al. 7634* (MO); Dtto. Acosta, Via Pilancones, 6 km of Mirimire, *Ruiz & Rondon 3726* (MY); Dtto. Colina, Río Ricoa, S of Las Dos Bocas, 200 m, 11°19′N, 69°24′W, *Steyermark & Gonzales 113632* (MO); Dtto, Zamora, Delta of Río Hueque, Coro–Morón, 100 km E of Coro, 50 m, *Bunting 7704* (cultivated; originally collected as *van der Werff 3522*) (MO, NY, VEN), *Croat 71734* (MO). MIRANDA: Carenero–Chirimena, 2 km NW of Carenero, 0–5 m, *Steyermark & Bunting 102313* (MO); Río Chupaquire, new road 1 km S of main road, S of El Guacuco, 7 km E of Cupira, 0–150 m, 10°09′N, 65°38′W, *Liesner & Gonzalez 11906* (MO, WIS), 11917 (MO); Dtto. Brion, Laguna Grande, 0–30 m, 10°33′N, 66°04′W, *Berry et al. 3740* (MO). ZULIA: Dtto. Mara, Río Guasare, near Destacamento Guasare No. 1 (La Yolanda), abajo del Destacamento, 200–250 m, *Bunting et al. 11993* (MO).

Anthurium watermaliense hort. ex L. Bailey & Nash, Stand. Cycl. Hort. 1:303. 1922. TYPE: Colombia. Not seen, introduced into horticulture via Watermall, Belgium. Neotype: Panama. Bocas del Toro: Changuinola–Almirante, Railroad Station Milla 7.5, less than 100 m, *Croat 38129* (lectotype MO-2820846; isoelectotypes, CAS, F, MEXU, NY, PMA, S, SEL, UC, US). Figures 333, 334.

Terrestrial; stem to 25 cm long, (1)1.5–3 cm diam.; roots numerous, descending, velutinous, 3–4 mm diam.; cataphylls thin, 4.5–14 cm long, obtuse to acute at apex, persisting as coarse linear fibers. *Leaves* erect-spreading; petioles (12)25–60(88) cm long, ca. 4–5 mm diam., subterete, flattened to slightly and narrowly sulcate with blunt to rounded margins adaxially, rounded abaxially; geniculum, 1–1.5 cm long; blades moderately coriaceous, ovate-triangular, long-acuminate at apex, deeply lobed at base, 21–60 cm long, (14)20–40 cm wide; anterior lobe 20–45 cm long; the posterior lobes mostly oblong, (7)14–26 cm long, (3.5)5–10(16) cm wide, rounded at apex; sinus parabolic to hippocrepiform; both surfaces semiglossy; midrib convexly raised above and below; basal veins 5–8 pairs, 2nd through 8th coalesced

4.5–8 cm, prominulous above and below; posterior rib mostly naked, weakly turned up on outer margin; primary lateral veins 4–8 per side, departing midrib at 40–45° angle, prominulous in grooves above, prominulous below; tertiary veins conspicuously raised below when dried; collective vein arising from 1st or 2nd basal vein, raised above and below, equally as prominent as primary lateral veins when dried, 3–6 mm from margin. *Inflorescences* spreading, shorter than leaves; peduncle (12)25–60(75) cm long, 3–7 mm diam., 0.5–1.5× as long as petiole; spathe erect to reflexed, subcoriaceous, usually dark violet-purple, sometimes green, lanceolate to ovate-lanceolate, 5–15(21) cm long, (1.5)2–6(8.5) cm wide, inserted at 75° angle on peduncle, long-acuminate at apex, acute to rounded (rarely cordate) and conspicuously decurrent at base; stipe 0.3–3 cm long; spadix white to greenish, yellow or purple, tapered, 7–19 cm long, 5–10 mm diam. near base, 2–5 mm diam. near apex; flowers rhombic to 4-lobed, 1.5–3.4 mm long, 1.8–3.1 mm wide, the sides straight to jaggedly sigmoid; 5–12 flowers visible in principal spiral, 6–16 in alternate spiral; tepals matte, punctate; lateral tepals 1.5–2.2 mm wide, the inner margins convex to ± straight; pistils raised, protruding beyond the stamens at anthesis, glossy, weakly exserted just before stamens emerged, dark green; stigma narrowly ellipsoid, ca. 0.5 mm long, droplets appearing 2–3 days before stamens emerge; stamens emerging rapidly from the base or sometimes in a scattered pattern throughout, held erect above the tepals; filaments translucent, exserted, 0.3–0.4 mm long, 0.6 mm wide; anthers creamy white, 0.9 mm long, 0.9–1 mm wide; thecae ellipsoid, divaricate; pollen white. *Infructescence* with spadix to 22 cm long, ca. 2 cm diam., bearing berries in the basal portion only; berries yellow to usually orange, ovoid to obovoid, shortly beaked at apex, 10–15 mm long, ca. 4–5 mm diam.

This species is known from Costa Rica and Panama, between sea level and 2,400 m; most collections have been made at about 750 m in premontane and lower montane rainforest. Populations occur near sea level in tropical moist and premontane wet forest. The species is extremely variable, especially in leaf size and shape, and spathe and spadix color.

Anthurium watermaliense can be recognized by its ovate-triangular leaf blades with pronounced posterior lobes (a unique feature within the section), its broad, decurrent and frequently dark purple spathe, tapered spadix with exserted stamens, and usually orange berries.

This species is most easily confused with specimens of *Anthurium cotobrusii*, which have unusually long posterior lobes, but the latter species differs in having the pistils shorter than the stamens at anthesis and stamens that do not persist exserted.

Anthurium watermaliense might also be confused with *A. standleyi*. See discussion of that species for distinguishing characters.

Although originally reported to have come from Colombia, no wild collections from present-day Colombia are known. Since Colombia encompassed Panama at the time of its introduction, it is believed that *A. watermaliense* was originally collected in Panama and may never be found in Colombia. In Panama, it has been found no further east than western Veraguas.

WITHOUT LOCALITY: *Drake 219* (P). COSTA RICA: WITHOUT FURTHER LOCALITY: *Lankester 349-49* (K). ALAJUELA: Monteverde, Chomogo trail and Refugio El Valle, 1,600 m, *Kennedy & Guindon 3799* (MO). CARTAGO: Palo Verde, beyond Quebrada Cangreja, 1,500 m, *Luteyn & Wilbur 4376* (MO); SE of Platanillo (Tsipiri), Raiz de Hule Camino, 1,200–1,300 m, *Croat 36713* (MO, PMA); 4.5 km S of bridge on Agua Caliente on Lourdes, ca. 8 km S of Cartago by air, Finca El Chaparral, 1,500 m, 9°49′N, 83°55′W, *Liesner & Judziewicz 14612* (MO); Quebrada Cangreja, 3 km S of Pan American Hwy., ca. 6 km S of Cartago by air, 1,620–1,650 m, 9°46′N, 83°57′W, *Liesner & Judziewicz 14455* (B, CR, MO, NY, RSA, WISC; Río Reventazón, CATIE, 3 km E of Turrialba "Los Espaveles" nature trail, 525–600 m, 9°54′N, 83°39′W, *Liesner et al. 15326* (MO); Tapantí Reserve, 1,400–1,700 m, *Goméz 19262* (MO). HEREDIA: Braulio Carrillo Park, Zurquí, 1,700–2,000 m, *Goméz 20220* (B, CR, K, MO, RSA); Cerro Zurquí, southern slope, 5 km N of San Luis Norte, 1,800 m, 10°03′N, 84°02′W, *Stolze 1548* (F, MO); Río San Rafael, Atlantic slope of Volcán Barva, 1,500 m, 10°13′N, 84°05′W, *Grayum 7021* (MBM, MO); between Río San Fernando and Río Sardinal, Atlantic slope of Volcán Barva, 1,850–1,880 m, 10°12′N, 84°06.5′W, *Grayum 7342* (MO). LIMÓN: Puerto Viejo de Cahuita–Manzanillo at Punta Mona, Panama border, 0–50 m, *Taylor & Skotak 4435* (DUKE, MO), *4529* (DUKE); range of hills 2 km S of Manzanillo de Talamanca, E of Quebrada Hone Wark, 190 m, 9°37′N, 82°39.5′W, *Grayum et al. 4393* (MO); Cordillera de Talamanca, Río Madre de Dios–Río Barbilla, Quebrada Cañabral, 280–400 m, *Grayum et al. 8839* (CR, MBM, MO); Reserva Biol. Hitoy Cerere Valle del Río La Estrella, 400 m, 9°40′15″N, 83°03′20″W, *Herrera & Chacón 2356* (CM, CR, MO); SE of Lago Dabagri, Telire, *Goméz et al. 23225* (CR, MO); Portete, 10 km N of Puerto Limón, 3 m, *Lent 347* (MO); Siquirres, Las Brisas de Pacuarito, 300 m, *Gomez et al. 23396* (MO, NY, US); Cerro Pirripli, just SE of Puerto Viejo de Talamanca, along trail from cemetery, 100–150 m, 9°39′N, 82°45′W, *Grayum 3631* (CR, MO, RSA); Río Catarata, Bribrí, less than 50 m, *Croat 43224* (CM, MO); Río Sixaola, 10–

50 m, 9°35′N, 82°53′E, *Burger et al. 10444* (F, MO). SAN JOSÉ–HEREDIA: Cerro Zurquí, southern slope, end of Calle Zurquí, 1,800–2,000 m, *Almeda & Nakai 3706* (MO); Río Para Blanca, Cerro de Zurquí, 1,600–1,800 m, 10°03′N, 84°01′W, *Burger et al. 9342* (MO). SAN JOSÉ: Carrillo Station, 700 m, *Gomez et al. 21168* (MEXU, MO). PANAMA. BOCAS DEL TORO: Changuinola–Almirante, Railroad Station at Milla 7.5, less than 100 m, *Croat 38129* (CAS, F, IBE, K, MEXU, MO, NY, PMA, RSA, S, SEL, UC, US, VDB, W, WIS), *Croat & Porter 16246* (MO); Criollo (just above Buena Vista)–Quebrada Higuerón, Chiriquí trail, *Kirkbride & Duke 784* (MO); 15 km S of town of Changuinola, Changuinola–1 dam site, 300–500 m, *Antonio 3146* (MO). CHIRIQUÍ: Quebrada Hondo–Continental Divide, on Calderas–Chiriquicito Trail, *Kirkbride & Duke 960* (MO); Boquete Region, Palo Alto, 4.5 mi. NE of Boquete, *Hammel 7542* (MO); Cerro Colorado, 1,200–1,500 m, *Croat 33265* (F, MO, SEL, US, VEN), *Folsom & Collins 1754, 1764* (MO), *Folsom et al. 4840* (MO), *Mori & Dressler 7849, 7852* (MO), *Sullivan 359* (MO); Cerro Colorado mine area, from Chamí station to 9 mi. along rd., 1,100–1,750 m, 8°35′N, 81°54′W, *Hammel & Trainer 14977* (MO); Fortuna Road, Gualaca–Fortuna Dam, 5.9 mi. NW of Los Planes de Hornito, 1,370 m, 8°43′N, 82°15′W, *Croat 49898* (MO). VERAGUAS: Santa Fe Region, N of Escuela Agrícola Alto Piedra, 700–900 m, *Croat 49035* (MO), *Croat & Folsom 33958* (CM, F, MO), *Folsom 2994* (MO), *Mori & Kallunki 2563* (MO); 6–7 km W of Santa Fe, 900 m, *Nee 9717* (MO, PMA).

Anthurium willifordii Croat, sp. nov. TYPE: Peru. Loreto: Napo River, Explorama Camp, on Río Sucusari, below 200 m (originally collected by Jack Williford), *Croat 61087* (holotype, MO 3244489; isotypes, B, K, NY, USM). Figures 339, 340.

Planta epiphytica; internodia brevia, 1–2 cm diam.; cataphyllum persistens intactum mox deciduum; petiolus quadrangularis ad trapeziformis, interdum subteres, 2–4.5 cm longus, 4–5 mm diam.; lamina oblanceolata aut oblanceolata-elliptica, (14)18–50 cm longa, 5.5–16 cm lata; nervis primariis lateralibus 6–13 utroque; pedunculus 2.5–9 cm longus; spatha erecta, atropurpureus, navicularis, 2.3–4 cm longa, 1–2 cm lata; spadix dilute purpureo-violaceum aut griseo-purpureum, cylindroideus, 1.7–4 cm longus, 2–5 mm diam.; baccae magentae.

Epiphytic; stem short, 1–2 cm diam.; roots numerous, dense, spreading to descending, pale to medium green, smooth, bluntly tapered, moderately elongate, 3–4 mm diam.; cataphylls subcoriaceous, broadly triangular, 1.5–5 cm long, acute at apex, pale yellowish green, drying brown, persisting intact, soon deciduous. *Leaves* spreading; petioles 2–4.5 cm long, 4–5 mm diam., erect-spreading to spreading, quadrangular to trapezoidal, sometimes subterete, with a medial rib and the margins prominently raised adaxially, sharply 3–5-ribbed abaxially, the surface slightly pale-speckled; geniculum becoming reddish tinged, 0.4–0.7 cm long; blades subcoriaceous to moderately coriaceous, oblanceolate to oblanceolate-elliptic, obtuse, minutely apiculate at apex, obtuse to rounded at base, (14)18–50 cm long, 5.5–16.5 cm wide, usually broadest above the middle, the margins sometimes undulate; upper surface matte-velvety, moderately quilted, medium green, lower surface velvety with conspicuous crystalline cells, slightly paler and often tinged with red; both surfaces drying brown to grayish brown; midrib prominently acute at base, becoming narrowly raised toward the apex above, prominently acute and tinged with reddish below; primary lateral veins 6–13 per side, departing midrib at 50–70° angle, straight, flat to weakly raised above, weakly raised and darker than surface and tinged with red below, drying slightly raised above and below; interprimary veins less prominent than primary lateral veins, darker than surface below; tertiary veins slightly darker than surface below, drying weakly raised; reticulate veins obscure; collective vein arising from near the base or in upper third of blade, weakly sunken to flat above, weakly raised and darker than surface below, equally as prominent as primary lateral veins, 4–10 mm from margin. *Inflorescences* erect; peduncle 2.5–9 cm long, 2–3 mm diam., 1.2–3× as long as petioles, green faintly tinged purplish, terete with obscure ridge; spathe erect, subcoriaceous, dark purple to purplish violet (B & K red-purple 2/5), ovate-elliptic, navicular, 2.3–4.7 cm long, 1–2 cm wide, broadest in the lower third, cuspidate-acuminate at apex, acute and weakly decurrent at base; spadix reddish (B & K red 7/10) to faintly purplish violet or grayish purple, very short, cylindroid, erect, 1.7–4.7 cm long, 2–6 mm diam.; flowers rhombic and weakly 4-lobed, 1–1.5 mm long, 1.5–1.7 mm wide, the sides ± straight parallel to spiral, jaggedly sigmoid perpendicular to spiral; 8–9(14) flowers visible in principal spiral, 17–21 in alternate spiral; tepals matte, densely and minutely papillate; lateral tepals 0.5–0.9 mm wide, the inner margins rounded to bluntly 3-sided, the outer margins 2–3-sided to shield-shaped and 4-sided; pistils raised, purple, much darker than the tepals; stigma slitlike, 0.2–0.3 mm long; stamens emerging from near the middle, lateral stamens emerging to ⅘ the distance to the apex before alternates emerge at lower ⅓ of spadix; anthers white, 0.4–0.5 mm long, 0.4–0.5 mm wide, contiguous at the surface of the tepals; thecae narrowly ovoid, conspicuously divaricate; pollen yellow, fading to white. *Infructescence* with berries scattered throughout; berries obovoid, magenta, rounded at apex.

Anthurium willifordii is endemic to Loreto Department in Peru, where it has been collected once in the vicinity of the Explorama Camp on the Río Sucusari, a tributary of the Río Napo, at less than 200 m. It was found here as an epiphyte in a tropical moist forest life zone.

This species is a very distinctive one, the chief characters being the short, stubby spadix on a short peduncle and the quilted leaf blades, which are matte above, velvety and frequently tinged red below. The petioles are of variable cross-sectional shape: quadrangular to trapezoidal or sometimes subterete; they are always sharply 3–5-ribbed abaxially.

No other species is likely to be confused with *A. willifordii*, and only *A. superbum* and *A. reflexinervium* share the character of quilted, velvety or red-tinged leaf blades.

The new species is named in honor of Jack Williford, of Brandon, Florida, who originally collected live plants along the Río Sucusari.

PERU. LORETO: Río Napo, Explorama Camp, on Río Sucusari, below 200 m, originally collected by Jack Williford, *Croat 61087* (B, K, MO, NY, USM).

Anthurium wurdackii Bunting, Acta Bot. Venez. 10: 279. 1975. TYPE: Venezuela. Amazonas: Cerro Yapacana, 3°45′N, 66°45′W, 825 m, *Steyermark & Bunting 103099* (holotype, VEN; isotypes, MO, MY, NY, US). Figure 341.

Description based on dried material only. Terrestrial or epilithic; stem short, stout, growing horizontally, 1.5–4 cm diam.; cataphylls thick, ca. 4–7 cm long, dark brown, persisting ± intact or weathering into fine linear fibers. *Leaves* erect to spreading; petioles 22–55 cm long, 5–8 mm diam., subterete, somewhat flattened and narrowly sulcate with rounded margins adaxially, rounded abaxially; geniculum 1–1.5 cm long; blades thickly coriaceous, broadly ovate-elliptic to somewhat broadly lanceolate in larger blades, acute to obtuse at apex, shallowly cordate at base, 28–53 cm long, 10.5–26 cm wide, broadest at or just below the middle; sinus broadly and shallowly arcuate; upper surface glossy, dark green, lower surface; midrib flat at base; becoming convexly raised toward apex; basal veins 3–4 pairs, prominently arcuate-ascending, usually merging with the margin, at least the first vein extending to near or above the middle of the blade; primary lateral veins 3–4 per side, departing midrib at 40–60° angle, slightly arcuate, steeply ascending, raised above and below; interprimary veins few, less conspicuous than primary lateral veins; tertiary veins sunken above, raised above and below; collective vein arising in the upper half of the blade or absent. *Inflorescences* longer than leaves; peduncle (44)55–81 cm long, ca. 4–7 mm diam., 1–2× as long as petiole; spathe erect-spreading at anthesis, becoming reflexed to recurled, subcoriaceous, green tinged with maroon at apex at anthesis, becoming purple, lanceolate, (6.5)8–14.5 cm long, 1.5–2.5 cm wide, decurrent for 1.5–2 cm at base; spadix maroon, stipitate to 7–13 mm, narrowly tapered, 6.5–18 cm long, 6–7 mm diam. near base, 3–4 mm diam. near apex; flowers rhombic, 2.7 mm long, 2.9 mm wide, the sides straight to weakly sigmoid; 8 flowers visible in principal spiral, 6 in alternate spiral. *Infructescence* with spathe persisting; spadix 7–21 cm long, 1.5–2 cm diam.; berries white, maroon at apex, ca. 8 mm diam.

Anthurium wurdackii is known only by two collections from Amazonas, Venezuela, on Cerro Yapacana at 825 m in premontane wet forest, and on Cerro Neblina at 780 m in lower montane moist forest.

This species is an atypical member of the section and can be recognized by its subterete petioles, coriaceous, broadly ovate-elliptic leaf blades that are shallowly cordate at the base and have three to four pairs of basal veins and steeply ascending, mostly free-ending primary lateral veins. Also characteristic are the long peduncle, maroon, sharply tapered spadix, and whitish berries that are maroon at the apex.

Anthurium wurdackii is not closely related to any other species in sect. *Pachyneurium*. In leaf texture, it is most similar to *A. bonplandii* subsp. *bonplandii* or subsp. *guayanum*, but those differ in lacking basal veins and having oblanceolate to elliptic leaf blades that are attenuate to obtuse at the base.

VENEZUELA. AMAZONAS: Cerro Yapacana, 825 m, *Steyermark & Bunting 103099* (MO, MY, NY, US, VEN); Dpt. Río Negro, Cerro Neblina, Camp IV, 15 km NNE of Pico Phelps, north branch of river in canyon, 780 m, 0°51′N, 65°57′W, *Liesner 16664* (B, MO).

Anthurium xanthoneurum Bunting, Phytologia 60(5): 298. 1986. TYPE: Venezuela. Amazonas: Dept. Río Negro, Cerro Aratitiyope, ca. 70 km SSW of Ocamo, 900 m, 2°10′N, 65°34′W, *Steyermark et al. 130054* (holotype, NY; isotypes, MO, VEN). Figure 342.

Description based on dried material only. Epilithic; stem short, ca. 2.5 cm diam. *Leaves* with petioles less than 10 cm long; geniculum thicker than petiole, 2.5 cm long; blades thickly coriaceous, oblanceolate-elliptic, obtuse at apex, obtuse to narrowly rounded at base, 30–55 cm long, 8.5–15 cm wide, broadest above the middle, the margins prominently revolute; upper surface semiglossy and weakly quilted, lower surface paler, matte and with conspicuous brown glandular punctations, yellow-green; midrib convexly raised above, more prominently so below; primary lateral veins 8–10 per side, departing midrib at 30–40° angle, weakly arcuate to the margin, convexly raised above in moderately deep grooves, conspicuously raised below; interprimary veins absent; tertiary veins prominulous, especially on the upper surface; collective vein absent. *Inflorescence* with peduncle 50 cm long, ca. 6 mm diam.; spathe unknown; spadix (post anthesis) brownish green, long-tapered, erect, 24 cm long, ca. 8 mm diam. near base, ca. 4 mm diam. near apex, broadest at the base.

Anthurium xanthoneurum is known only from the type collection from Cerro Aratitiyope in Amazonas, Venezuela, at 990 m in a premontane rainforest life zone.

This species is distinguished by its heavily coriaceous leaf blades with steeply ascending primary lateral veins, and its slender, long-tapered spadix.

Anthurium xanthoneurum is closely related to *A. bonplandii* and especially resembles subsp. *guayanum*. That taxon differs, however, in having mostly broader leaf blades with the primary lateral veins ascending at a wider angle.

VENEZUELA: AMAZONAS: Dpt. Río Negro. Cerro Aratitiyope, 70 km SSW of Ocamo, streams feeding Río Manipitare, 990–1,670 m, 2°10′N, 65°34′W, *Steyermark et al. 130054* (NY, VEN).

EXCLUDED SPECIES

Anthurium aduncum (Vell. Conc.) Schott, Prod. Aroid. 478. 1860. TYPE: Brazil. Illustration in Vellozo (1825). (Fl. Flum. Tab. 124 serves as the type.)

This species is based on an illustration (*Pothos aduncus*) in Vellozo's Flora Fluminensis (1825). Schott (1865) transferred it to *Anthurium* and included it in his section *Pachyneurium*. Engler (1905) placed the name among his "Species dubia." There are only two *Pachyneurium* species known from southern Brazil, *A. coriaceum* G. Don in Sweet and *A. solitarium* (Vell. Conc.) Schott, and *A. aduncum* does not look remotely like either of them. The narrow blades with numerous veins indicate that it is most likely a member of sect. *Urospadix*. Its exact affinities may never be known, since that group has many similar species.

Anthurium agnatum Schott, Oesterr. Bot. Z. 8: 181. 1858. TYPE: Nicaragua. *Oersted s.n.* Type destroyed. (Field Museum photo 29807 serves as the type.)

This species, included in sect. *Pachyneurium* by both Schott (1860) and Engler (1905), was based on a sterile *Oersted* collection from Nicaragua. Although reported by Engler to be at Copenhagen, no such specimen exists there today. This may have been in error, because an *Oersted* collection bearing the name *Anthurium agnatum* was photographed (Field Museum 29807) at the Vienna herbarium (W), before the latter was destroyed during World War II. Schott also prepared an illustration of the same specimen (Schott illustration 468, Fiche 15:610). The photograph of the specimen and the Schott illustration are all that exist today.

The leaf blades of *Anthurium agnatum* are shaped like those of *A. spathiphyllum* N. E. Br., but have fewer than 10 primary lateral veins (vs. 20–30 for the latter). It may be an unusual specimen of *A. bradeanum* Croat & Grayum, a species similar to *A. spathiphyllum*, but that species, though possessing fewer primary lateral veins, has ovate-elliptic blades less than five times longer than broad. The blades of the *Oersted* collection are narrowly oblanceolate and over six times longer than broad. The unavailability of a specimen for examination of leaf texture, coloration, and venation makes it impossible to identify it with certainty, so it remains a nomen dubium.

Anthurium andicola Liebm., Vidensk. Meddel. Dansk Naturahist. Floren. Kiobenhavn 1: 22. 1849. TYPE: Mexico. Veracruz: Santa María Alpatlahua, 2,500 m, *Liebmann s.n.* (lectotype, K).

Designated as a *Pachyneurium* by Engler (1905), but rejected due to its lack of involute vernation, this species is a member of sect. *Belolonchium* (*A. andicola* Alliance); see Croat (1983).

Anthurium brownii Masters, Gard. Chron. 11. 744. 1876. TYPE: Colombia. Valle: vic. Buenaventura, *Wallis s.n.* (type, K).

This species was included in sect. *Pachyneurium* by Engler (1905), but it lacks involute vernation. It is possibly a member of sect. *Belolonchium*.

Anthurium cartilagineum (Desf.) Kunth, Enum. Pl. 3: 79. 1879. TYPE: Venezuela. (Schott Drawings 678-680 serve as the type.)

Included in sect. *Pachyneurium* by Engler (1905), but lacking involute vernation. Section unknown.

Anthurium cordatum (Willd.) G. Don in Sweet, Hort. Brit. 633. 1839. TYPE: West Indies, Willdenow Herbarium Cat. Nr. 3101 (type, B).

Included in sect. *Pachyneurium* by Engler (1905), but lacking involute vernation. Section unknown.

Anthurium cuspidatum Masters, Gard. Chron. I. 428. 1875. TYPE: Colombia?, Hort. Vietch, Jan. 1875 (K).

This species was erroneously included under sect. *Pachyneurium* in my revision of *Anthurium* for Mexico and Middle America (Croat, 1983), based on a misidentified plant with involute vernation. It is a member of sect. *Polyneurium*.

Anthurium grandifolium (Jacq.) Kunth, Enum. Pl. 3: 77. 1841. TYPE: Jamaica (erroneously reported as from Venezuela), Jacquin type not seen. (Willendow Herbarium specimen 3102 (B) might serve as the type if the Jacquin specimen is not located.)

This species was included in sect. *Pachyneurium* by Engler (1905), but rejected due to the presence of supervolute rather than involute vernation. Section unknown.

Anthurium hacumense Engl., Bot. Jahrb. Syst. 25. 363. 1898. TYPE: Costa Rica. Puntarenas: of Río Hacum, near Buenos Aires, 250 m, *Tonduz 6536* (holotype, B; isotypes, BR, CR).

Like *Anthurium hookeri* (see below), *A. hacumense* has glandular-punctate blades. Having overlooked the glandular punctations, Engler no doubt placed the species in *Pachyneurium* owing to its large size and rosulate habit; it is a typical member of sect. *Porphyrochitonium*.

Anthurium hookeri Kunth, Enum. Pl. 3: 74. 1841. TYPE: Schott Drawing 517 serves as the lectotype (designated by Mayo 1982).

Though treated as a *Pachyneurium* by both Schott (1860) and Engler (1905), *Anthurium hookeri* does not belong there. It differs from all species of *Pachyneurium* by having supervolute vernation and leaf blades with scalariform secondary venation and glandular punctations on the lower blade surface. It probably belongs to its own section or is an unusual member of sect. *Porphyrochitonium*.

Anthurium lilacinum Bunting, Acta Bot. Venez. 10: 273. 1975. TYPE: Venezuela. Carabobo: headwaters of Río San Gian, above Los Tanques and La Toma, S of Barburata, 750–900 m, *Steyermark 95294* (holotype, VEN; isotype, MY).

Anthurium lilacinum was erroneously reported as a member of sect. *Pachyneurium* by Croat and Lambert (1986). This was based on its rosulate habit and otherwise superficial resemblance to species of this section. Later studies revealed it to lack involute vernation. It is probably a member of sect. *Urospadix*.

Anthurium longispathum Carriere, Rev. Hort. 498. 1888. TYPE: Guadeloupe (based on cultivated collection, no type specimen prepared ?).

The species was treated by Engler (1905) as a *Pachyneurium*. It is a synonym of *Anthurium grandifolium* (Jacq.) Kunth (see that species).

Anthurium maximum (Desf.) Engl., Pflanzenr. IV. 23B(Heft 21): 77. 1905. TYPE: No specimen or illustration pertaining to the type is known.

Anthurium maximum was described by Desfontaines in 1829 in *Pothos*. Schott did not deal with the name at all, but Engler (1879) treated it as a synonym of *A. fontanesii* in his first treatment of *Anthurium*. In his 1905 revision, Engler correctly transferred *Pothos maxima* to *Anthurium* and treated *A. fontanesii* as a synonym of *A. maximum*. Desfontaines' brief description compares the plant with *Pothos crassinervia* Jacq. from which it was said to differ by its larger blade "broadened toward the apex, its longer, sulcate petiole and its longer spadix." Engler may have seen some preserved material of *A. maximum*, perhaps a specimen at the Paris Herbarium pre-

pared by Desfontaines. However, if any such collection ever existed, there is no longer any record of it. Engler's description of *A. maximum* closely matches Schott's original description of *A. fontanesii*, now considered a synonym of *A. crassinervium*, but the vague nature of *A. maximum* precludes making any definitive treatment, and it is treated here as a nomen dubium.

Anthurium michelii Guillaumin, Bull. Mus. Hist. Nat. (Paris) 31: 263. 1925. TYPE: Panama. Bocas del Toro: hills beyond Fish Creek Lagoon, *Wedel 2276* (holotype, P).

This species was erroneously reported as a *Pachyneurium* by Croat (1983), and it was later suggested (Croat, 1986) to be a member of sect. *Urospadix*. However, the latter group is probably restricted to eastern South America and has less conspicuous primary lateral veins. *Anthurium michelii* is not a *Pachyneurium* owing to its supervolute vernation and is perhaps best placed in a new, unnamed section with *A. decurrens* (see discussion in Introduction).

Anthurium seleri Engl., Bot. Jahrb. Syst. 25: 459. 1898. TYPE: Guatemala. Huehuetenango, vic. Chacula, *Seler 2643* (holotype, B).

This species was included in *Pachyneurium* by Engler (1905), but it lacks involute vernation. It is probably a member of sect. *Belolonchium* (*A. andicola* Alliance).

Anthurium tricarinatum Sodiro, Ant. Ecuator. Adiciones 1. 1903. TYPE: Ecuador. Cañar: valley of Río Cañar, *Rimbach 81* (type lost).

Though a well described species, *Anthurium tricarinatum* cannot be assigned with certainty to any known section. Sodiro compared it with *A. leonianum*, a very typical *Pachyneurium*, but he also said the leaves were black-punctate on the lower surface, a feature most closely associated with sect. *Porphyrochitonium*. Engler (1905) treated the species as a *Pachyneurium*, but his description appears to be based on that of Sodiro, and there is no way to be sure that he ever saw a specimen. Unless a specimen or a photograph of the Rimbach specimen becomes available, the species is best considered a nomen dubium.

Anthurium weberbaueri Engl., Pflanzenr. IV. 23B(Heft 21): 81. 1905. TYPE: Peru. Sandia, 2,100–2,300 m, *Weberbauer 543* (holotype, B; isotype, G).

This species was included in *Pachyneurium* by Engler (1905), but belongs in sect. *Digitinervium* by virtue of its scalariform veins and glandular punctations.

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APPENDIX 1. Taxonomic status of species included in Schott's grex *Pachyneurium* (1860).*

55	*A. wagenerianum* K. Koch & Bouché	
56	*A. recusatum* Schott	= *A. fendleri* Schott
57	*A. fendleri* Schott	
58	*A. brachygonatum* Schott	= *A. schlechtendalii* Kunth
59	*A. spectabile* Schott	
60	*A. huegelii* Schott	= *A. hookeri* Kunth
61	*A. mexicanum* Liebm.	= *A. schlechtendalii* Kunth
62	*A. rugosum* Schott	= *A. crassinervium* (Jacq.) Schott
63	*A. crassinervium* Schott	= *A. crassinervium* (Jacq.) Schott
64	*A. hookeri* Kunth	Not sect. *Pachyneurium*
65	*A. affine* Schott	
66	*A. ellipticum* K. Koch	= *A. crassinervium* (Jacq.) Schott
67	*A. tetragonum* Hook.	= *A. schlechtendalii* Kunth
68	*A. egregium* Schott	= *A. crassinervium* (Jacq.) Schott
69	*A. schlechtendalii* Kunth	
70	*A. acaule* Schott	= *A. acaule* (Jacq.) Schott
71	*A. dombeyanum* Brongn. ex Schott	= *A. dombeyanum* Brongn. ex Schott
72	*A. agnatum* Schott	Nomen dubium
73	*A. solitarium* Schott	
74	*A. aduncum* Schott	= *A. aduncum* (Vell. Conc.) Schott section *Urospadix*?

* The numbers are those used by Schott.

APPENDIX 2. Taxonomic status of species included in Engler's sect. *Pachyneurium* (1905).*

7	*A. pendulifolium* N. E. Br.	
8	*A. paraguayense* Engl.	
9	*A. preussii* Engl.	= *A. crasinervium* (Jacq.) Schott
10	*A. joseanum* Engl.	= *A. protensum* Schott
11	*A. wagenerianum* K. Koch & Bouché	
12	*A. ellipticum* K. Koch & Bouché	= *A. crassinervium* (Jacq.) Schott
13	*A. acaule* sensu Schott (1860) & Engl. (1905) non (Jacq.) Schott	= *A. crenatum* Kunth
14	*A. recusatum* Schott	= *A. fendleri* Schott
15	*A. hookeri* Kunth	not sect. *Pachyneurium*
16	*A. jenmanii* Engl.	
17	*A. trinitatis* Engl.	= *A. jenmanii* Engl.
18	*A. tenuispadix* Engl.	= *A. uleanum* Engl.
19	*A. brachygonatum* Schott	= *A. schlechtendalii* Kunth
20	*A. buenaventurae* Engl.	= *A. fendleri* Schott
21	*A. uleanum* Engl.	
22	*A. tarapotense* Engl.	
23	*A. cubense* Engl.	
24	*A. glaziovii* Hook.f.	= *A. solitarium* (Vell. Conc.) Schott
25	*A. hacumense* Engl.	sect. *Porphyrochitonium*
26	*A. strictum* N. E. Br.	= *A. oxycarpum* Poeppig
27	*A. tetragonum* Hook. ex Schott	= *A. schlechtendalii* Kunth
28	*A. schlechtendalii* Kunth	
29	*A. crassinervium* (Jacq.) Schott	
30	*A. maximum* (Desf.) Engl.	Nomen dubium (See Excluded Species)
31	*A. leonianum* Sodiro	
32	*A. acutifolium* Engl.	
33	*A. rugosum* Schott	= *A. crassinervium* (Jacq.) Schott
34	*A. affine* Schott	
34a	*A. latissimum* Engl.	
35	*A. cymatophyllum* K. Koch & Sellow	Nomen dubium (See Excluded Species)
36	*A. barclayanum* Engl.	
37	*A. ernestii* Engl.	
38	*A. agnatum* Schott	Nomen dubium (See Excluded Species)
39	*A. kunthianum* Liebm.	= *A. schlechtendalii* Kunth
40	*A. nobile* Engl.	= *A. solitarium* (Vell. Conc.) Schott
41	*A. dombeyanum* Brongn.	= *A. dombeyanum* Brongn. ex Schott
41a	*A. rigidissimum* Engl.	= *A. dombeyanum* Brongn.
42	*A. fortinense* Engl.	= *A. schlechtendalii* Kunth
43	*A. tricarinatum* Sodiro	Nomen dubium (See Excluded Species)
44	*A. weberbaueri* Engl.	sect. *Digitinervium*
45	*A. fendleri* Schott	
46	*A. rusticum* N. E. Br. ex Engl.	= *A. paraguayense* Engl.
47	*A. salviniae* Hemsley	
48	*A. spectabile* Schott	
49	*A. lindmanianum* Engl.	
50	*A. martianum* K. Koch & Kolb	
51	*A. selloum* K. Koch	
52	*A. longispathum* Carriere	= *A. grandifolium* (Jacq.) Kunth
53	*A. grandifolium* (Jacq.) Kunth	Not sect. *Pachyneurium*
54	*A. boucheanum* K. Koch	= *A. cartilagineum* (Desf.) Kunth
55	*A. liebmannii* Schott	= *A. umbrosum* Liebm.
56	*A. umbrosum* Liebm.	Not sect. *Pachyneurium*
57	*A. cordatum* (Willd.) G. Don	Not sect. *Pachyneurium*
58	*A. andicola* Liebm.	Not sect. *Pachyneurium*
59	*A. cartilagineum* (Desf.) Kunth	Not sect. *Pachyneurium*
60	*A. brownii* Masters	Not sect. *Pachyneurium*
61	*A. appunianum* Schott	= *A. cartilagineum* (Desf.) Kunth
62	*A. seleri* Engl.	Not sect. *Pachyneurium*

* The numbers are those used by Engler. Those with letter subscripts were treated at the end of the revision.

APPENDIX 3. Species of *Pachyneurium* (including placement in Schott (1860) and Engler (1905) where applicable).

Croat revision	Schott	Engler
acutifolium Engl.		x
var. *acutifolium*		
var. *herrerae* Croat		
**acutissimum* Engl.		sect. *Urospadix* Engl.
affine Schott	x	x
**angustilaminatum* Engl.		sect. *Urospadix* Engl.
subsp. *angustilaminatum*		
*subsp. *cibuserpentis* Croat		
anorianum Croat		
asplundii Croat		
atropurpureum R. Schultes & Maguire		
var. *arenicola* Croat		
var. *atropurpureum*		
var. *thomasii* Croat		
barclayanum Engl.		x
basirotundum Croat		
bonplandii Bunting		
subsp. *bonplandii* Bunting		
subsp. *cuatrecasii* Croat		
subsp. *guayanum* (Bunting) Croat		
bradeanum Croat & Grayum		
brenesii Croat & R. A. Baker		
bucayanum Croat		
bushii Croat		
campii Croat		
**carchiense* Croat		
cataniapoense Croat		
caucavallense Croat		
colonicum K. Krause		
concolor K. Krause		
consobrinum Schott	grex *Oxycarpium*	sect. *Episeiostenium* Schott
coriaceum G. Don in Sweet	grex *Acamptophyllium*	sect. *Urospadix* Engl.
cotobrusii Croat & R.A. Baker		
cowanii Croat		
crassinervium (Jacq.) Schott	x	x
crenatum (L.) Kunth		as *A. acaule* (Jacq.) Schott sensu Schott
cubense Engl.		x
curtispadix Croat		
dombeyanum Brongn. ex Schott	x	x
ernestii Engl.		x
var. *ernestii*		
var. *oellgaardii* Croat		
eximium Engl.		sect. *Epsieiostenium* Schott
**fasciale* Sodiro		
fatoense K. Krause		
fendleri Schott	x	x
galactospadix Croat		
glaucospadix Croat		
guanchezii Bunting		
halmoorei Croat		
hammelii Croat		
harlingianum Croat		
**holmnielsenii* Croat		
iramirezae Bunting		
jenmanii Engl.		x

APPENDIX 3. Continued.

Croat revision	Schott	Engler
johnsoniae Croat		
knappiae Croat		
krukovii Croat		
lanjouwii Jonker & Jonker		
latissimum Engl.		x
lennartii Croat		
leonianum Sodiro		x
lindmanianum Engl.		x
linguifolium Engl.		sect. *Urospadix* Engl.
llewelynii Croat		
loretense Croat		
luteynii Croat		
machetioides Matuda		
maguirei A. Hawkes		
manabianum Croat		
manuanum Croat		
martianum K. Koch & Kolb		x
**napeaum* Engl.		sect. *Urospadix* Engl.
**narinoense* Croat		
nervatum Croat		
nizandense Matuda		
**obscurinervium* Croat		
oerstedianum Schott	x	sect. *Urospadix* Engl.
**ottonis* K. Krause		
oxycarpum Poeppig & Endl.	grex *Oxycarpium*	sect. *Oxycarpium* Schott
**oxyphyllum* Sodiro		sect. *Urospadix* Engl.
pachylaminum Croat		
**palenquense* Croat		
**pallatangense* Croat		
paraguayense Engl.		x
var. *coroicoanum* Croat		
var. *paraguayense*		
pendulifolium N. E. Br.		x
**penningtonii* Croat		
plowmanii Croat		
pranceanum Croat		
prolatum Croat & R. A. Baker		
protensum Schott	grex *Erythropodium*	sect. *Urospadix* Engl.
subsp. *arcuatum* Croat		
subsp. *protensum*		
pseudospectabile Croat		
purpureospathum Croat		
ranchoanum Engl.		sect. *Calomystrium* Schott
reflexinervium Croat		
remotigeniculatum Croat		
salvadorense Croat		
salviniae Hemsley		x
**santiagoense* Croat		
sarukhanianum Croat & Haager		
schlechtendalii Kunth	x	x
subsp. *jimenezii* (Matuda) Croat		
subsp. *schlechtendalii*		
schottianum Croat & R. A. Baker		
seibertii Croat & R. A. Baker		
selloum K. Koch		x
simpsonii Croat		

APPENDIX 3. Continued.

Croat revision	Schott	Engler
solitarium (Vell. Conc.) Schott	x	as *A. affine* Schott
solomonii Croat		
**soukupii* Croat		
sparreorum Croat		
spathiphyllum N. E. Br.		sect. *Episeiostenium*
spectabile Schott	x	x
standleyi Croat & R. A. Baker		
superbum Madison		
subsp. *brentberlinii* Croat		
subsp. *superbum*		
tarapotense Engl.		x
tenaense Croat		
uleanum Engl.		x
var. *nanayense* Croat		
var. *uleanum*		
upalaense Croat & R. A. Baker		
validifolium K. Krause		
vaupesianum Croat		
venosum Griseb.		sect. *Cardiolonchium* Schott
vinillense Bunting		
wagenerianum K. Koch & Bouché	x	x
watermaliense hort ex L. Bailey & Nash		
willifordii Croat		
wurdackii Bunting		
xanthoneurum Bunting		

* Those species marked to the left with an asterisk are members of series *Multinervia*. All others are members of series *Pachyneurium*.

An x in the column under Schott or Engler indicates that the species was included in their respective systems.

APPENDIX 4. *Pachyneurium* geographical checklist.

	Mexico	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Colombia	Ecuador	Peru	Bolivia	Venezuela	Guyana	Surinam	Fr. Guiana	Brazil	Paraguay	Argentina	West Indies
acutifolium																				
var. *acutifolium*							O	X												
var. *herrerae*							O													
acutissimum										O										
affine																	O			
angustilaminatum																				
subsp. *angustilaminatum*										O										
subsp. *cibuserpentis*										O										
anorianum									O											
asplundii										O										
atropurpureum																				
var. *atropurpureum*									O		X						X			
var. *arenicola*									X	O	X	X					X			
var. *thomasii*												O								
barclayanum										O	X									
basirotundum											O									
bonplandii																				
subsp. *bonplandii*									X				O				X			
subsp. *cuatrecasii*									X				O							
subsp. *guayanum*													O		X					
bradeanum	X	X	O																	
brenesii		O																		
bucayanum										O										
bushii										O										
campii										O										
carchiense									X	O										
cataniapoense													O				X			

APPENDIX 4. Continued.

	Mexico	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Colombia	Ecuador	Peru	Bolivia	Venezuela	Guyana	Surinam	Fr. Guiana	Brazil	Paraguay	Argentina	West Indies
caucavallense									O											
colonicum								O												
concolor								O	X											
consobrinum						O	X	X												
coriaceum																	O			
cotobrusii							X	O												
cowanii														O						
crassinervium									X				O							X
crenatum																				O
cubense			X			X	X	X	X				X							O
curtispadix										O										
dombeyanum										X	O									
ernestii																				
var. *ernestii*									X	X	O						X			
var. *oellgaardii*										O										
eximium							O													
fasciale										O										
fatoense							X	O												
fendleri								X	X				O							
galactospadix									X		X						O			
glaucospadix									O											
guanchezii													O							
halmoorei	O																			
hammelii								O												
harlingianum									X	O										
holmnielseni										O										
iramirezae													O							
jenmanii													X	O	X	X	X			X

APPENDIX 4. Continued.

	Mexico	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Colombia	Ecuador	Peru	Bolivia	Venezuela	Guyana	Surinam	Fr. Guiana	Brazil	Paraguay	Argentina	West Indies
johnsoniae									O											
knappiae											O									
krukovii																	O			
lanjouwii															O					
latissimum											O									
lennartii										O										
leonianum										O										
lindmanianum																	O			
linguifolium										O										
llewelynii											O									
loretense									X	X	O						X			
luteynii								O												
machetioides	O																			
maguirei															O					
manabianum										O										
manuanum											O									
martianum														O						
napaeum									X	O										
narinoense									O											
nervatum								O												
nizandense	O																			
obscurinervium										O										
oerstedianum							O													
ottonis											X	O								
oxycarpum									X	X	O	X					X			
oxyphyllum										O										
pachylaminum											O									
palenquense										O										
pallatangense										O										
paraguayense																				
var. *coroicoanum*											X	O								
var. *paraguayense*												X					X	O		X

APPENDIX 4. Continued.

	Mexico	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Colombia	Ecuador	Peru	Bolivia	Venezuela	Guyana	Surinam	Fr. Guiana	Brazil	Paraguay	Argentina	West Indies
pendulifolium									O	X	X									
penningtonii										O	X									
plowmanii											X	X					O	X		
pranceanum																	O			
prolatum							O	X												
protensum																				
subsp. *arcuatum*							X	O												
subsp. *protensum*							O	X												
pseudospectabile								O												
purpureospathum								O												
ranchoanum							O	X												
reflexinervium											O									
remotigeniculatum											O									
salvadorense			X	O																
salviniae	X		O		X	X	X	X	X											
santiagoense										O										
sarukhanianum	O																			
schlechtendalii																				
subsp. *jimenezii*	O																			
subsp. *schlechtendalii*	O	X	X		X	X														
schottianum							O													
seibertii							X	O												
selloum																				O
simpsonii											O									
solitarium																	O			
solomonii												O								
soukupii										X	O	X								
sparreorum										O										
spathiphyllum							X	X	X											
spectabile							O													
standleyi							O													

APPENDIX 4. Continued.

	Mexico	Belize	Guatemala	El Salvador	Honduras	Nicaragua	Costa Rica	Panama	Colombia	Ecuador	Peru	Bolivia	Venezuela	Guyana	Suriname	Fr. Guiana	Brazil	Paraguay	Argentina	West Indies
superbum																				
subsp. *brentberlinii*											○									
subsp. *superbum*										○										
tarapotense											○									
tenaense										○										
uleanum																				
var. *nanayense*											○									
var. *uleanum*									X	X	X						○			
upalaense						X	○													
validifolium							X	○												
vaupesianum									○											
venosum																				○
vinillense													○							
wagenerianum													○							X
watermaliense							X	X												
willifordii											○									
wurdackii													○							
xanthoneurum													○							
Total # of taxa	7	1	4	1	2	7	23	23	24	36	28	9	14	3	4	1	18	2	1	7
Types	6	0	1	1	0	1	13	11	8	29	18	4	12	3	2	0	9	1	0	4
Endemics	5	0	0	0	0	0	7	5	6	23	13	2	5	2	2	0	6	0	0	3

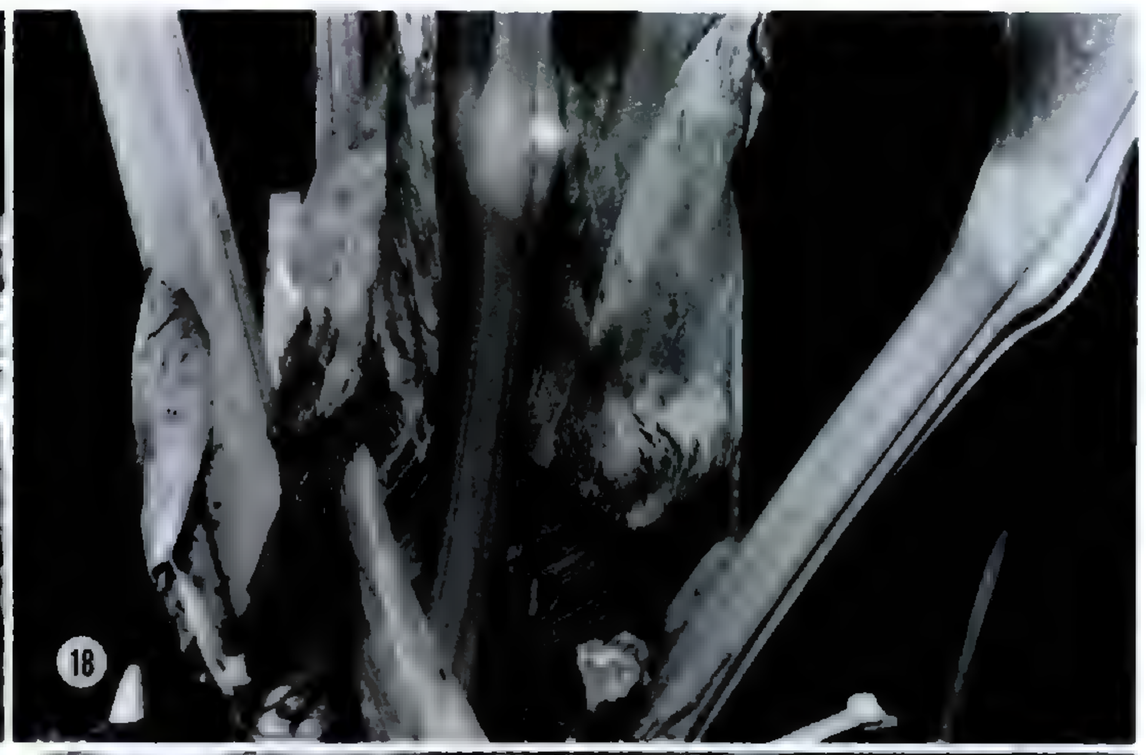
Note: circles refer to the type locality, X's refer to any other country where the species occurs.

FIGURES 1–4.—1. *Anthurium cubense* Engl., *Neill 2730*, showing involute vernation.—2. *A. hacumense* Engl., showing convolute vernation.—3. *A. michelii* Guill., Panama: Fortuna, *Croat & Grayum 60252*, showing *Pachyneurium*-like habit.—4. *A. harrisii* (Graham) Endl., *Croat 38340*, showing *Pachyneurium*-like habit.

FIGURES 5–8.—5. *Anthurium hacumense* Engl., *Croat 33558*, showing *Pachyneurium*-like habit.—6. *A. hookeri* Kunth, cultivated, *Virden s.n.*, showing convolute vernation and *Pachyneurium*-like habit.—7. *Anthurium harlingianum* Croat, *Croat 50816*, showing erect, debris-trapping roots (internodes obscured by roots).—8. *A. asplundii* Croat, cultivated at Selby Bot. Gard. (*SEL 82-265*), showing new flush of roots.

FIGURES 9–12.—9. *Anthurium pendulifolium* N. E. Br., cultivated by Burle-Marx, showing semi-intact cataphyll and downward-growing roots.—10. *A. asplundii* Croat, *Croat 55586*, showing dense roots, severed petioles & hook-shaped cataphylls.—11. *A. dombeyanum* Schott, *Croat 50919* showing straight, lanceolate, intact cataphylls.—12. *A. sparreorum* Croat, *Croat 57195*, cultivated by T. Fennel, Homestead, Florida, showing weathered cataphylls.

FIGURES 13–16.—13. *Anthurium dombeyanum* Schott, *Croat 58323*, showing debris-covered roots.—14. *A. barclayanum* Engl., *Croat 50712*, showing debris-trapping roots.—15. *A. salviniae* Hemsley, *Croat 32786*, showing cucullate cataphyll.—16. *A. harlingianum* Croat, cultivated at Selby Bot. Gard., *Croat 67410*, showing hook-shaped cataphyll.



FIGURES 17–20.—17. *Anthurium loretense* Croat, *Croat 51226*, showing circinate vernation.—18. *A. luteynii* Croat, *Croat 25521*, showing mostly intact cataphylls.—19. *A. sparreorum* Croat, *Croat 38666*, showing intact and weathered cataphylls.—20. *A. salviniae* Hemsley, Panama: Barro Colorado Island (not collected), showing variation in leaf blade base shape.

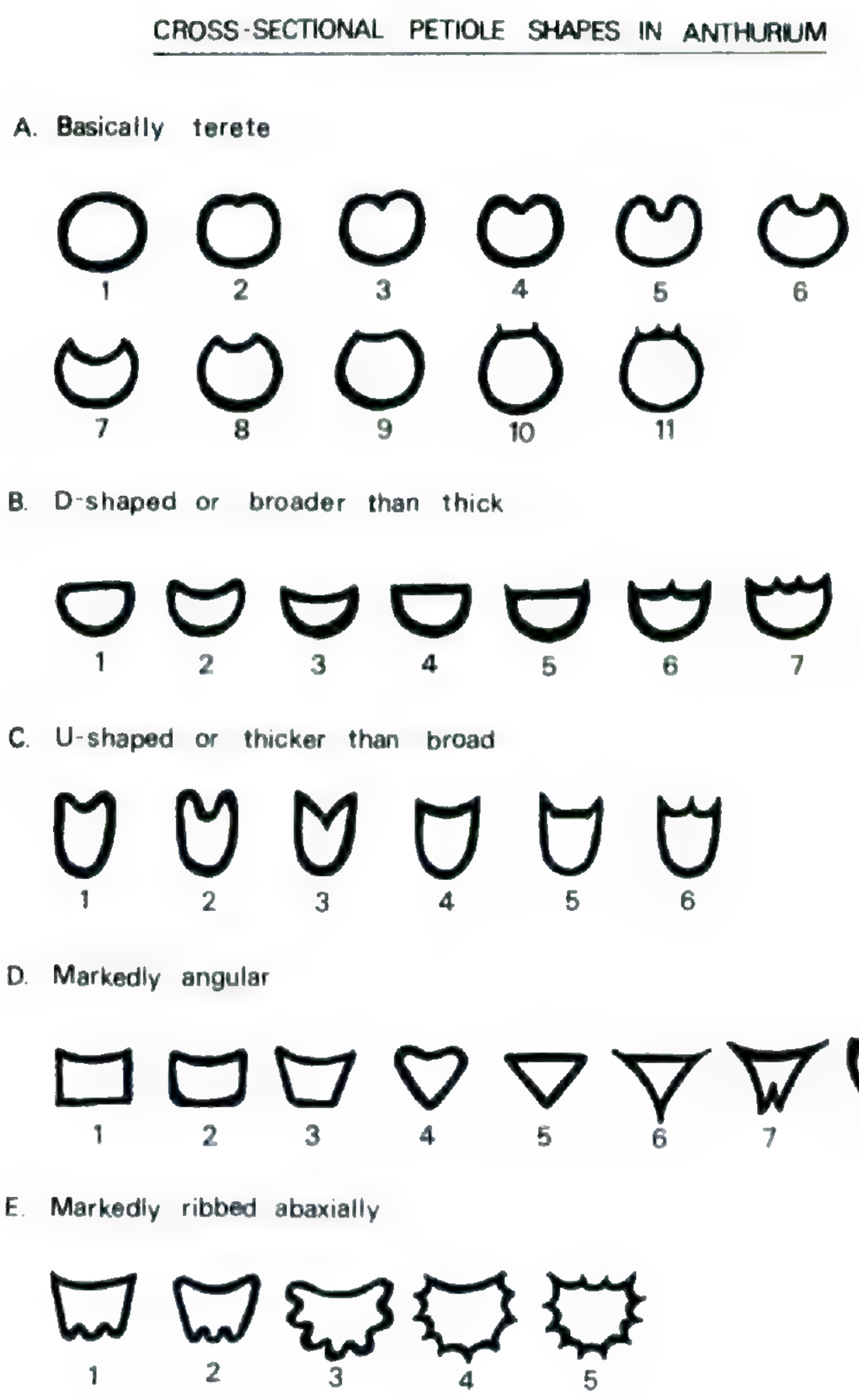


FIGURE 21. Cross-sectional petiole shapes in *Anthurium*.—A. Basically terete: ranging from esulcate (1), to shallowly and acutely sulcate (2 & 3), to obtusely and broadly sulcate (4), to narrowly and obtusely sulcate (5), to narrowly and acutely sulcate (6), broadly and acutely sulcate (7), shallowly and broadly sulcate (8), flat adaxially (9), flat adaxially with marginal ribs (10), to flat adaxially with marginal and medial ribs (11).—B. D-shaped or broader than thick: ranging from flat adaxially with obtuse margins (1), to broadly sulcate with obtuse margins (2), broadly sulcate with acute margins (3), flat adaxially with acute margins (4), flat adaxially with erect margins (5), to flat adaxially with erect margins and with 1 or more medial ribs (6 & 7).—C. U-shaped or thicker than broad: ranging from broadly and obtusely sulcate (1) to narrowly and obtusely sulcate (2), narrowly and acutely sulcate with acute margins (3), shallowly and acutely sulcate (4), sulcate with acute margins (5), to sulcate with sharp margins and a medial rib (6).—D. Markedly angular: ranging from quadrangular with acute angles (1), to quadrangular with obtuse angles (2), trapezoidal (3), obtusely triangular (4), acutely triangular (5), acutely triangular with 2 marginal ribs (6), basically triangular with two abaxial ribs (7), obtusely triangular, narrowly and sharply sulcate with convex sides (8).—E. Markedly ribbed abaxially: ranging from trapezoidal or quadrangular, sharply and broadly sulcate adaxially, 3-ribbed abaxially (1), to obtusely and broadly sulcate adaxially, 3-ribbed abaxially (2), broadly and obtusely sulcate adaxially, 5-ribbed abaxially (3), broadly and sharply sulcate adaxially, narrowly and sharply ribbed around the remaining circumference (4), or with one or more ribs on the sulcus (5).

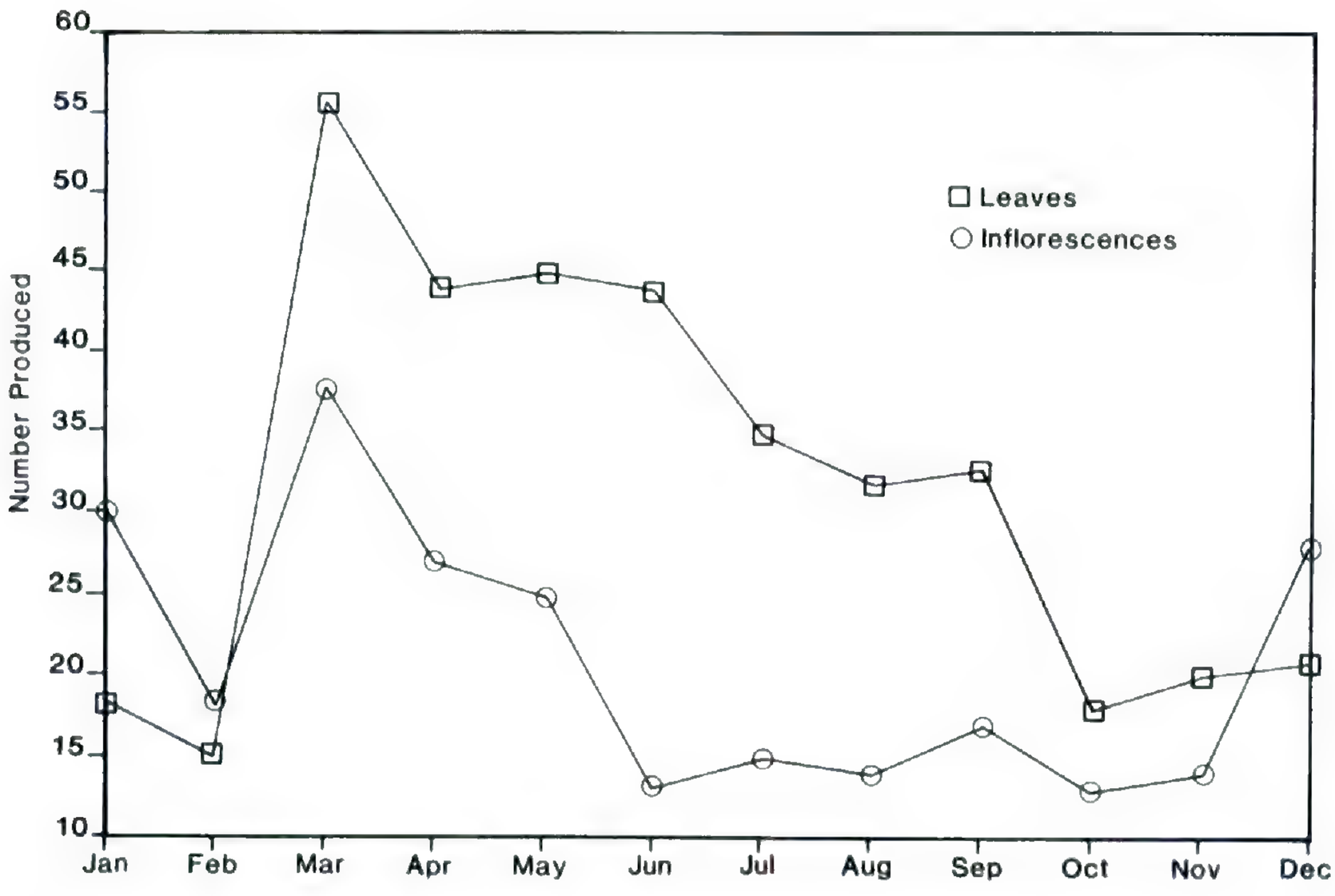
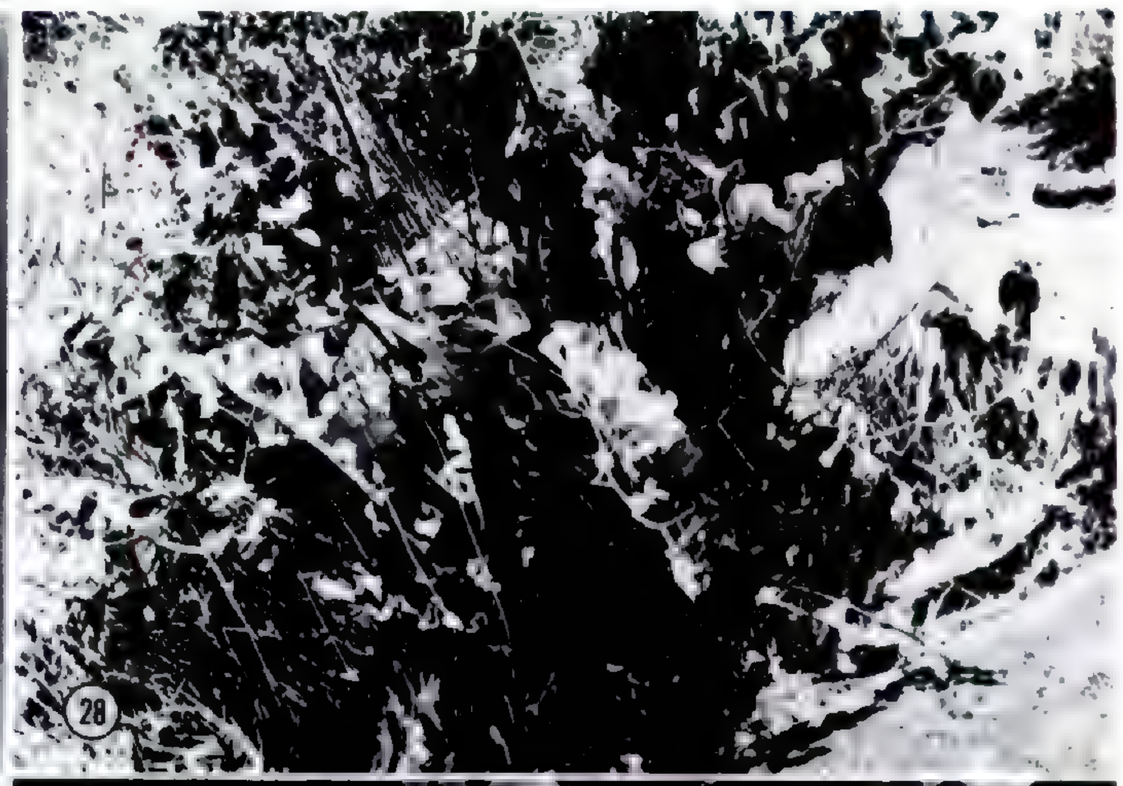


FIGURE 22. Graph illustrating inflorescence and leaf production over 2-year period.

FIGURES 23–26.—23. *Anthurium acutifolium* Engl., *Pittier 4099*.—24–25. *A. acutissimum* Engl., *Madison 2094*.—26. *A. affine* Schott, *Storr 194* (cultivated at Kew).



FIGURES 27–30.—27. *Anthurium acutifolium* Engl., *Croat 59853*.—28–29. *A. affine* Schott, *Hahn s.n.* (photo by B. Hahn).—30. *A. anorianum* Croat, *Croat 56757*.

FIGURES 31–34.—31. *Anthurium angustilaminatum* Engl. subsp. *angustilaminatum*, *Sodiro s.n.*—32. *A. angustilaminatum* Engl. var. *cibuserpentis* Croat, *Steyermark 53764.*—33, 34. *A. anorianum* Croat, *Croat 56757.*

FIGURES 35–38.—35, 36. *Anthurium asplundii* Croat, *Croat 50693*.—37. *A. asplundii* Croat, *Croat 55586*.—38. *A. atropurpureum* R. Schultes & Maguire var. *atropurpureum*, *Croat 56927*.

FIGURES 39–42.—39. *Anthurium atropurpureum* R. Schultes & Maguire var. *arenicola* Croat, *Croat 50303*.—40, 41. *A. atropurpureum* R. Schultes & Maguire var. *arenicola* Croat, cultivated at Selby Bot. Gard. (*SEL 78-1146*).—42. *A. atropurpureum* R. Schultes & Maguire var. *arenicola* Croat, *Croat 53698*.

FIGURES 43–46.—43. *Anthurium asplundii* Croat, *Croat 55608.*—44. *A. atropurpureum* R. Schultes & Maguire var. *atropurpureum*, *Croat 56927.*—45. *A. atropurpureum* R. Schultes & Maguire var. *arenicola* Croat, *Croat 53582.*—46. *A. barclayanum* Engl., *Croat 50702.*

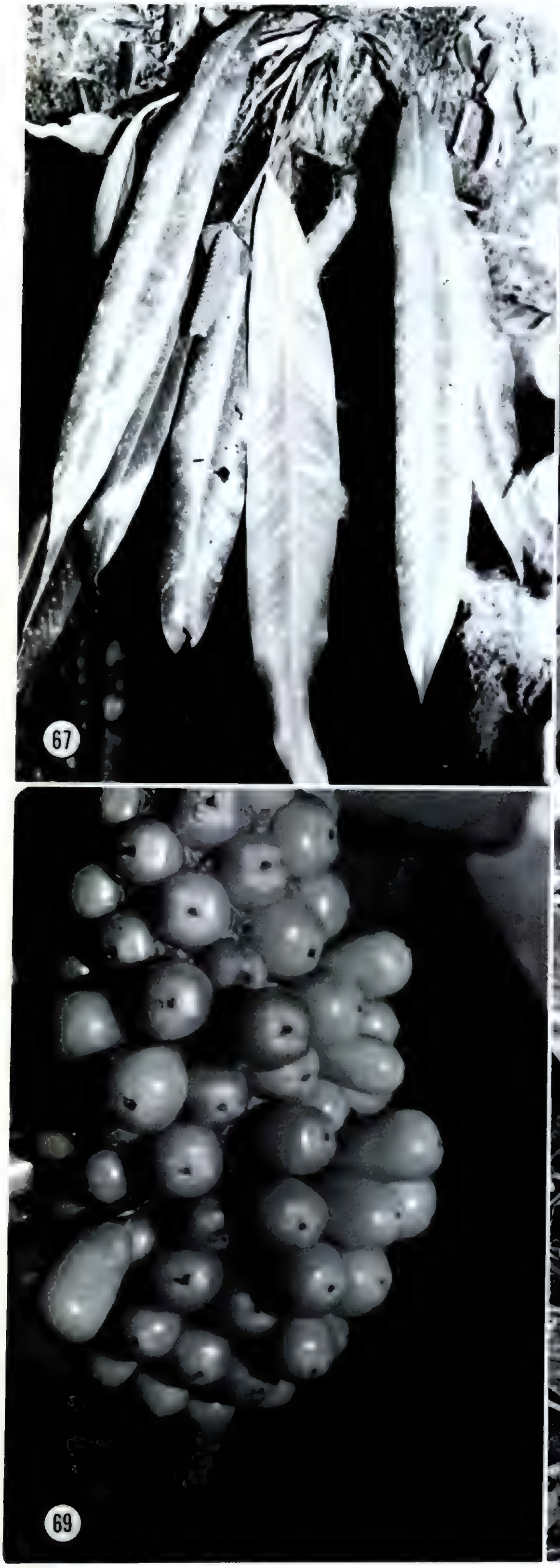
FIGURES 47–50.—47–49. *Anthurium barclayanum* Engl., *Croat 50702*.—50. *A. basirotundum* Croat, *Plowman 5980A*.

FIGURES 51–54.—51, 52. *Anthurium basirotundum* Croat, *Plowman 5980A.*—53. *A. bonplandii* Bunting subsp. *bonplandii, Croat 59326.*—54. *A. bonplandii* Bunting subsp. *bonplandii, Croat 59260.*

FIGURES 55–58.—55. *Anthurium bonplandii* Bunting subsp. *bonplandii*, *Croat 59260*.—56–58. *A. bonplandii* Bunting subsp. *cuatrecasii* Croat, *Croat 55065*.

FIGURES 59–62.—59. *Anthurium barclayanum* Engl., *Thompson 373*.—60–62. *A. bonplandii* Bunting subsp. *guayanum* (Bunting) Croat, *Croat 54062*.

FIGURES 63–66.—63. *Anthurium bradeanum* Croat & Grayum, *Croat 35751*.—64. *A. bradeanum* Croat & Grayum, *Croat 36480A*.—65. *A. brenesii* Croat & R. A. Baker, *Croat 46923*.—66. *A. bucayanum* Croat, *Croat 61597*.



FIGURES 67–70.—67–69. *Anthurium brenesii* Croat & R. A. Baker, *Croat 46923*.—70. *A. bucayanum* Croat, *Croat 50912*.

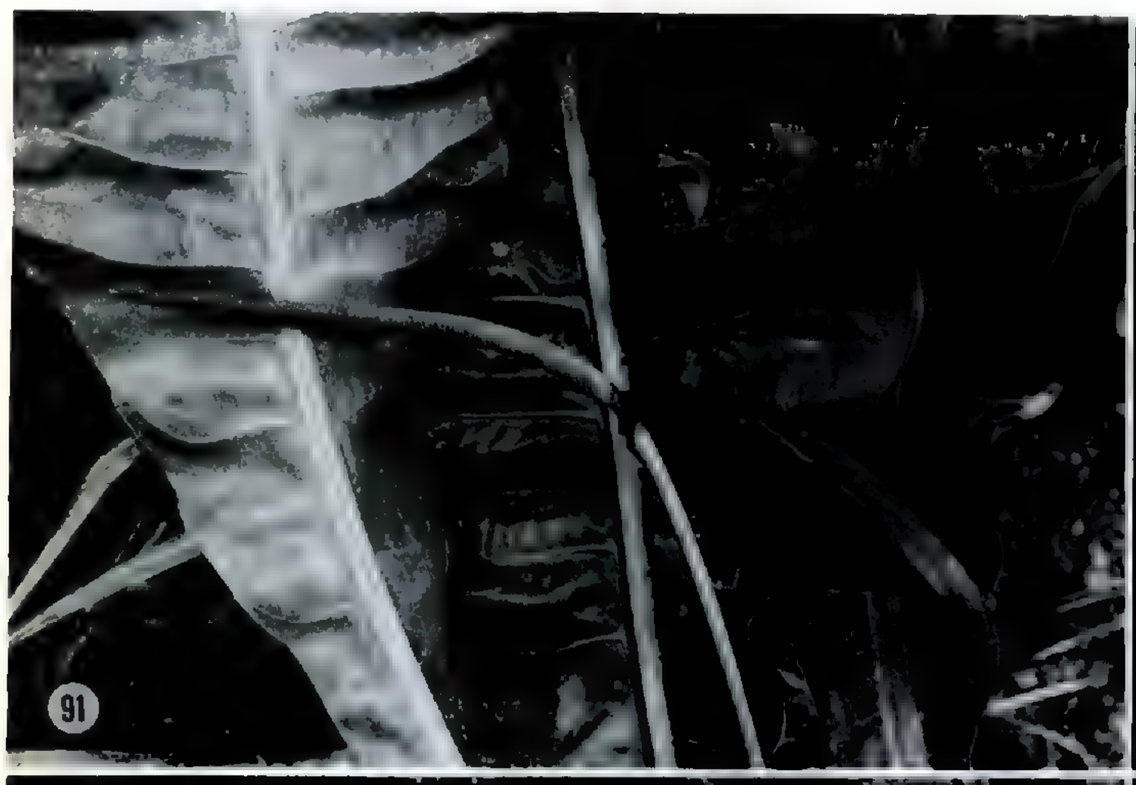
FIGURES 71–74.—71–72. *Anthurium bucayanum* Croat, *Croat 61597*.—73. *A. bushii* Croat, *Madison et al. 3285*.—74. *A. campii* Croat, *Croat 61562*.

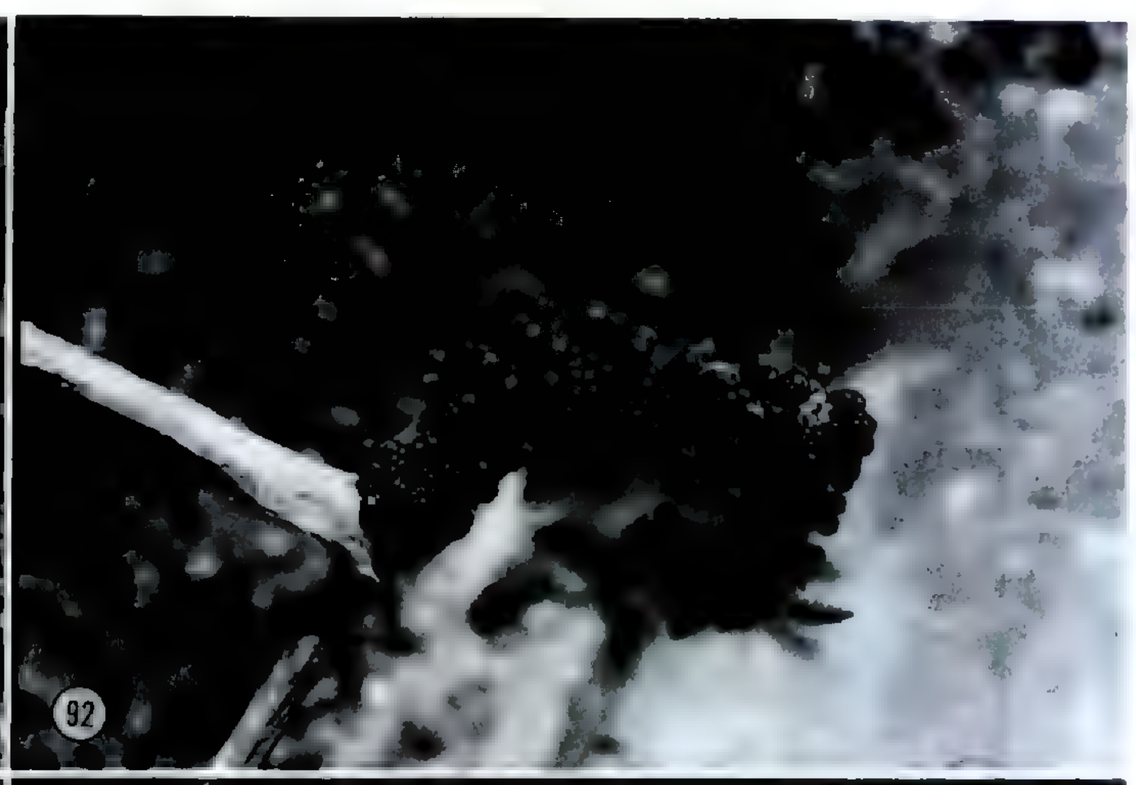
FIGURES 75–78.—75, 76. *Anthurium campii* Croat, *Croat 61562*.—77, 78. *A. carchiense* Croat, *Madison 3998*.

FIGURES 79–82.—79–80. *Anthurium campii* Croat, *Croat 61562.*—81. *A. carchiense* Croat, *Madison 3998.*—82. *A. cataniapoense* Croat, *Croat 59319.*

FIGURES 83–86.—83–85. *Anthurium cataniapoense* Croat, *Croat 59319*.—86. *A. caucavallense* Croat, *Croat 56729*.

FIGURES 87–90.—87. *Anthurium caucavallense* Croat, *Croat 56729.*—88. *A. colonicum* K. Krause, *Croat 25831*, specimen destroyed.—89. *A. colonicum* K. Krause, *Croat 33640.*—90. *A. concolor* K. Krause, *Croat 33637.*





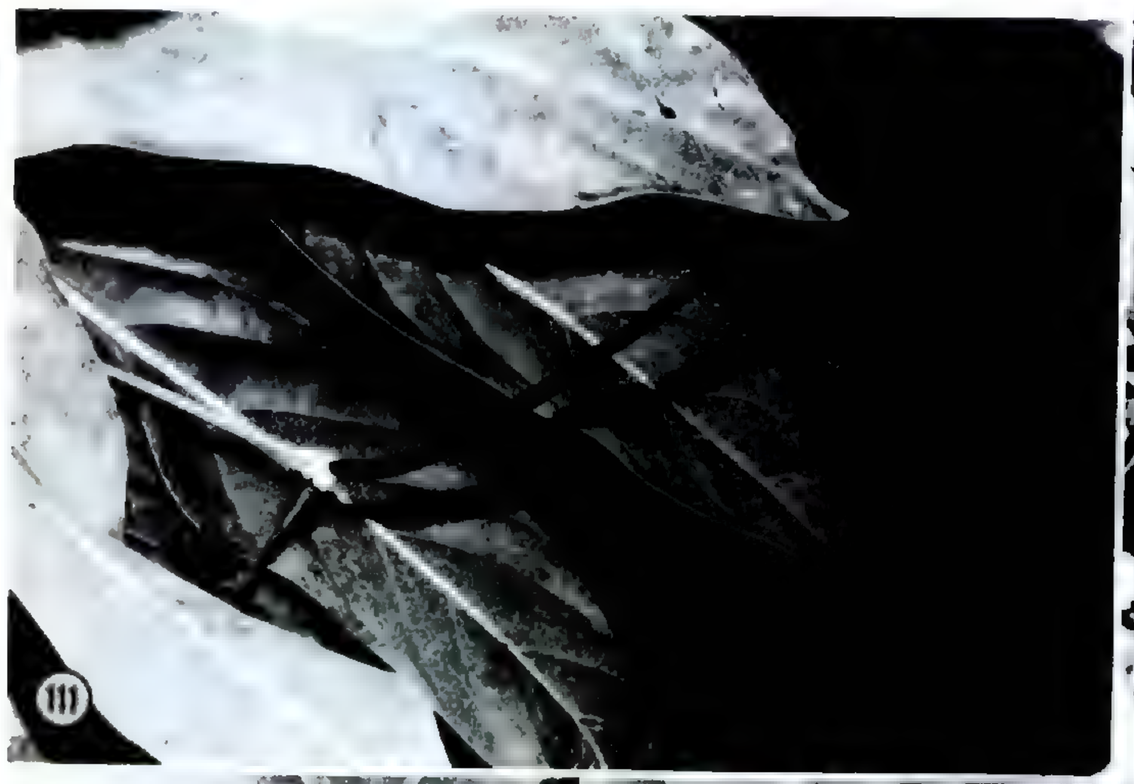
FIGURES 91–94.—91, 92. *Anthurium caucavallense* Croat, *Croat 56729*.—93. *A. colonicum* K. Krause, *Croat 33519*.—94. *A. concolor* K. Krause, *Croat 33637*.

FIGURES 95–98.—95, 96. *Anthurium concolor* K. Krause, *Croat 33637*.—97. *A. coriaceum* G. Don in Sweet, *Croat 53757*.—98. *A. coriaceum* G. Don in Sweet, cultivated by Burle-Marx.

FIGURES 99–102.—99, 100. *Anthurium consobrinum* Schott, cultivated at Las Cruces Bot. Gard. (#*75-375*).—101. *A. consobrinum* Schott, *Burger & Baker 151*.—102. *A. coriaceum* G. Don in Sweet, cultivated at Prague.

FIGURES 103–106.—103. *Anthurium cowanii* Croat, *Cowan & Soderstrom 1758.*—104. *Anthurium crassinervium* (Jacq.) Schott, *Croat 60621.*—105. *A. crassinervium* (Jacq.) Schott, *Croat 38338.*—106. *A. crenatum* (L.) Kunth, cultivated at Kew.

FIGURES 107–110.—107. *Anthurium cotobrusii* Croat & R. A. Baker, *Croat 67983*.—108. *A. cotobrusii* Croat & R. A. Baker, *Croat 33058*.—109. *A. crassinervium* (Jacq.) Schott, Venezuela: Jardin Botánico de Caracas (not collected).—110. *A. crassinervium* (Jacq.) Schott, *Croat 60621*.



FIGURES 111–114.—111. *Anthurium crenatum* (L.) Kunth, cultivated at Kew.—112. *A. cubense* Engl., Venezuela: Zulia (photo: Bunting).—113. *A. cubense* Engl., *Neill 2730*.—114. *A. curtispadix* Croat, *Croat 55207*.

FIGURES 115–118.—115. *Anthurium crenatum* (L.) Kunth, cultivated at Kew.—116, 117. *A. cubense* Engl., *Neill 2730.*—118. *A. curtispadix* Croat, *Croat 55207.*

FIGURES 119–122.—119. *Anthurium dombeyanum* Brongn. ex Schott, Peru: Machupicchu (photo by T. Plowman).—120, 121. *A. dombeyanum* Brongn. ex Schott, *Croat 58366*.—122. *A. dombeyanum* Brongn. ex Schott, *Croat 50847*.

FIGURES 123–126.—123. *Anthurium curtispadix* Croat, *Croat 55207*.—124. *A. ernestii* Engl. var. *ernestii*, *Croat 50993*.—125. *A. eximium* Engl., *Croat 67622*.—126. *A. fasciale* Sodiro, cultivated at Munich Bot. Gard. (#*83/2905*; photo: Bogner).

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FIGURES 127–130.—127. *Anthurium dombeyanum* Brongn. ex Schott, *Croat 58324*.—128. *A. ernestii* Engl. var. *ernestii*, *Croat 50994*.—129. *A. ernestii* Engl. var. *ernestii*, *Croat 50993*.—130. *A. ernestii* Engl. var. *ernestii*, *Croat 58591*.

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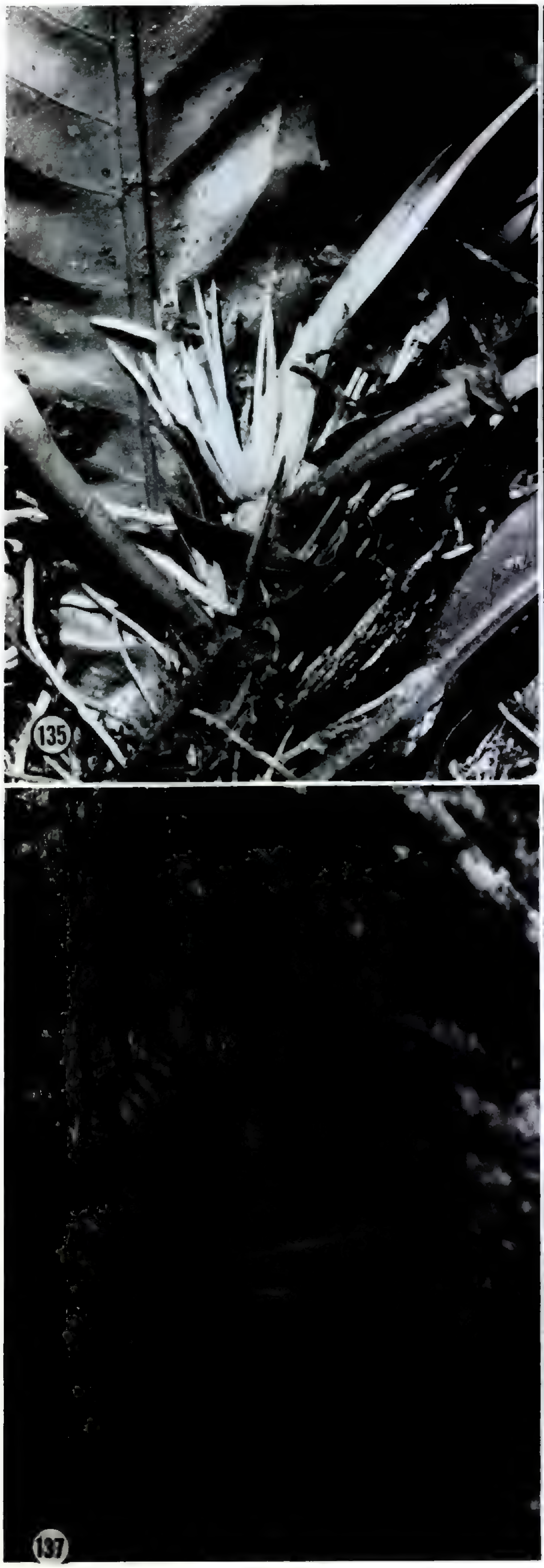
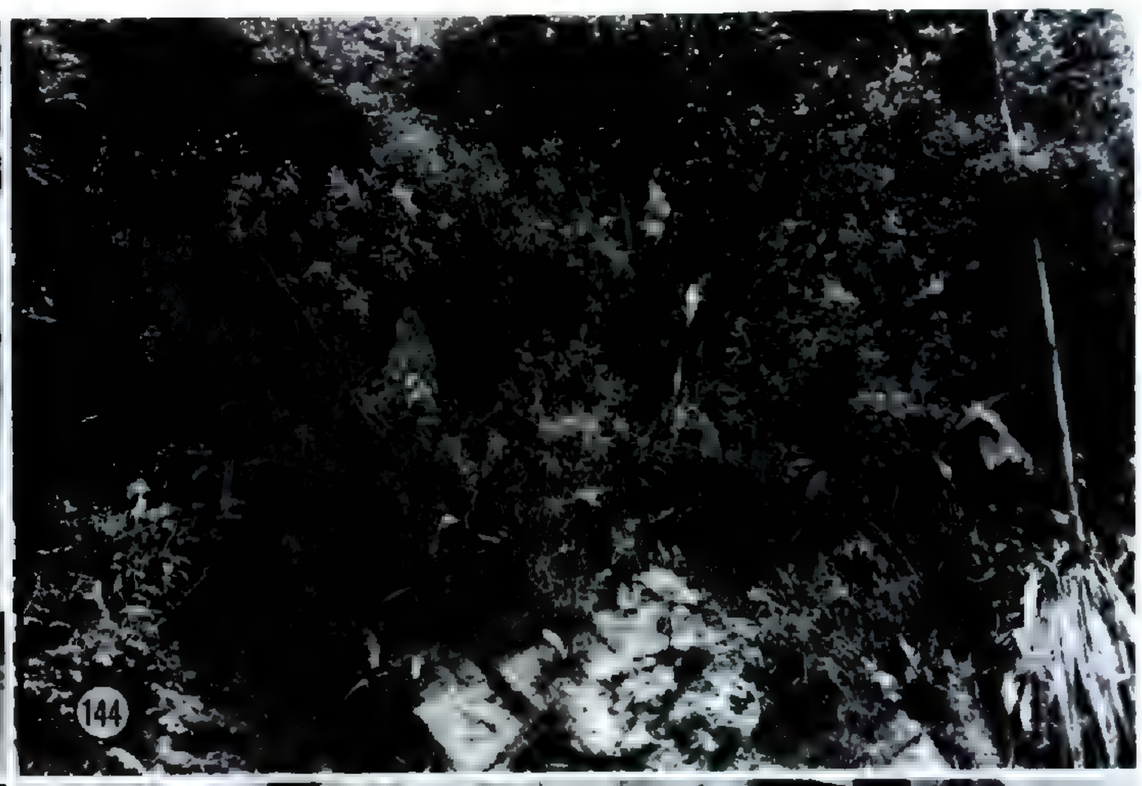
FIGURES 131–134.—131. *Anthurium ernestii* Engl. var. *oellgaardii* Croat, *Oellgaard et al. 34801.*—132. *A. eximium* Engl., *Croat 57240.*—133. *A. fasciale* Sodiro, cultivated at Munich Bot. Gard. (#*83/2905*; photo: Bogner).—134. *A. fatoense* K. Krause, *Croat 57229.*



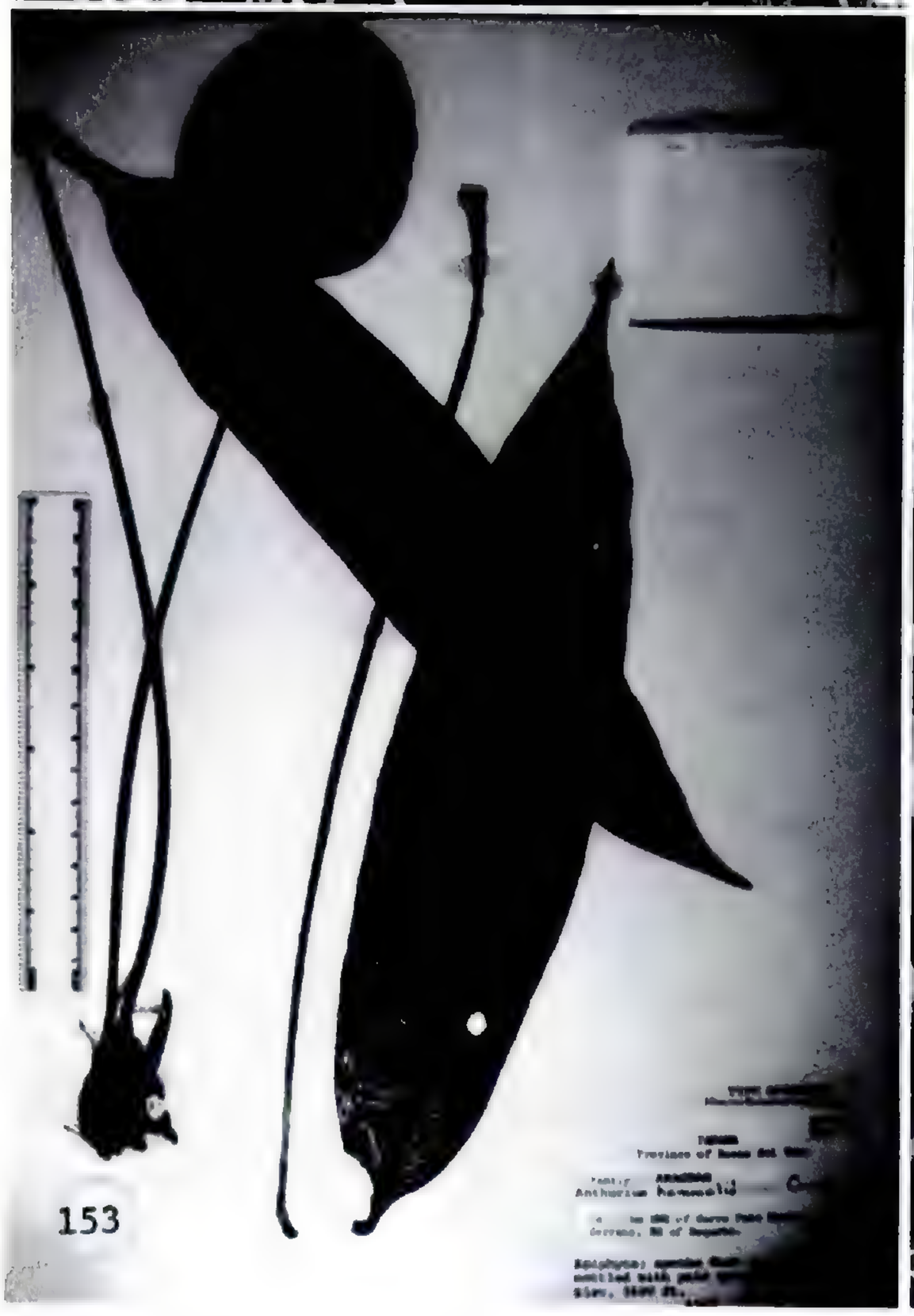
FIGURES 135–138.—135. *A. fatoense* K. Krause, *Croat 49893*.—136. *A. fatoense* K. Krause, *Folsom 2949*.—137. *A. fendleri* Schott, *Croat 54612*.—138. *A. fendleri* Schott, cultivated by Bette Waterbury.

FIGURES 139–142.—139. *Anthurium fendleri* Schott, *Croat 56578*.—140. *A. galactospadix* Croat, cultivated by Burle-Marx.—141, 142. *A. glaucospadix* Croat, *Croat 56753*.



FIGURES 143–146.—143. *Anthurium galactospadix* Croat, cultivated by Burle-Marx.—144. *A. glaucospadix* Croat, *Croat 56753*.—145. *A. glaucospadix* Croat, *Croat 52000*.—146. *A. halmoorei* Croat, *Croat 45337*.

FIGURES 147–150.—147. *Anthurium halmoorei* Croat, *Croat 45337*.—148. *A. hammelii* Croat, *Hammel 6160* (photo: Hammel).—149. *A. harlingianum* Croat, Ecuador: Pastaza (not collected).—150. *A. harlingianum* Croat, *Croat 49688*.



FIGURES 151–154.—151. *Anthurium glaucospadix* Croat, *Croat 57518.*—152. *A. halmoorei* Croat, *Croat 45337.*—153. *A. hammelii* Croat, *Hammel 6160.*—154. *A. harlingianum* Croat, *Croat 49688.*

FIGURES 155–158.—155. *Anthurium harlingianum* Croat, *Croat 50290.*—156, 157. *A. holmnielsenii* Croat, *Croat 61640.*—158. *A. jenmanii* Engl., *Hay 2827.*

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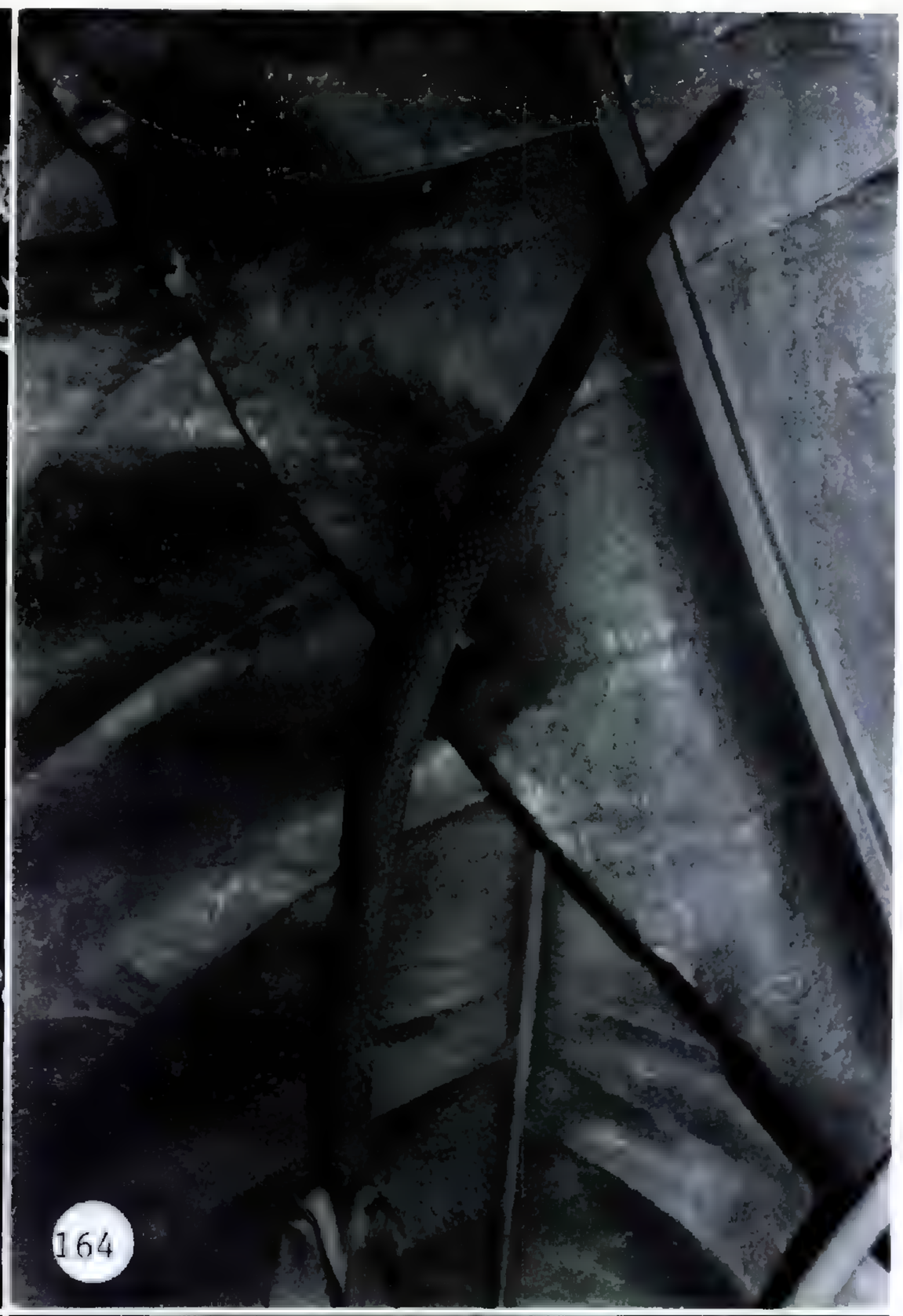
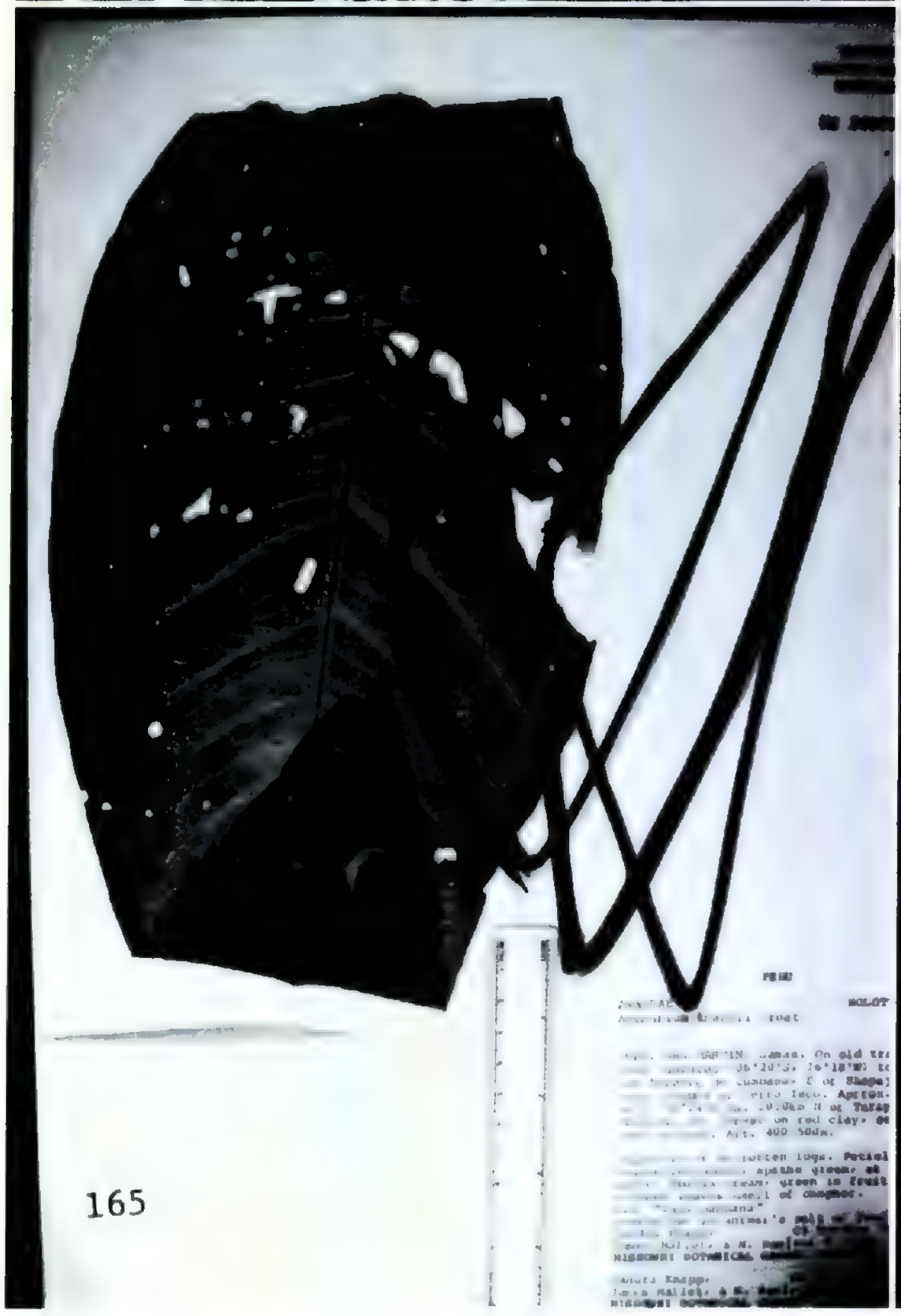
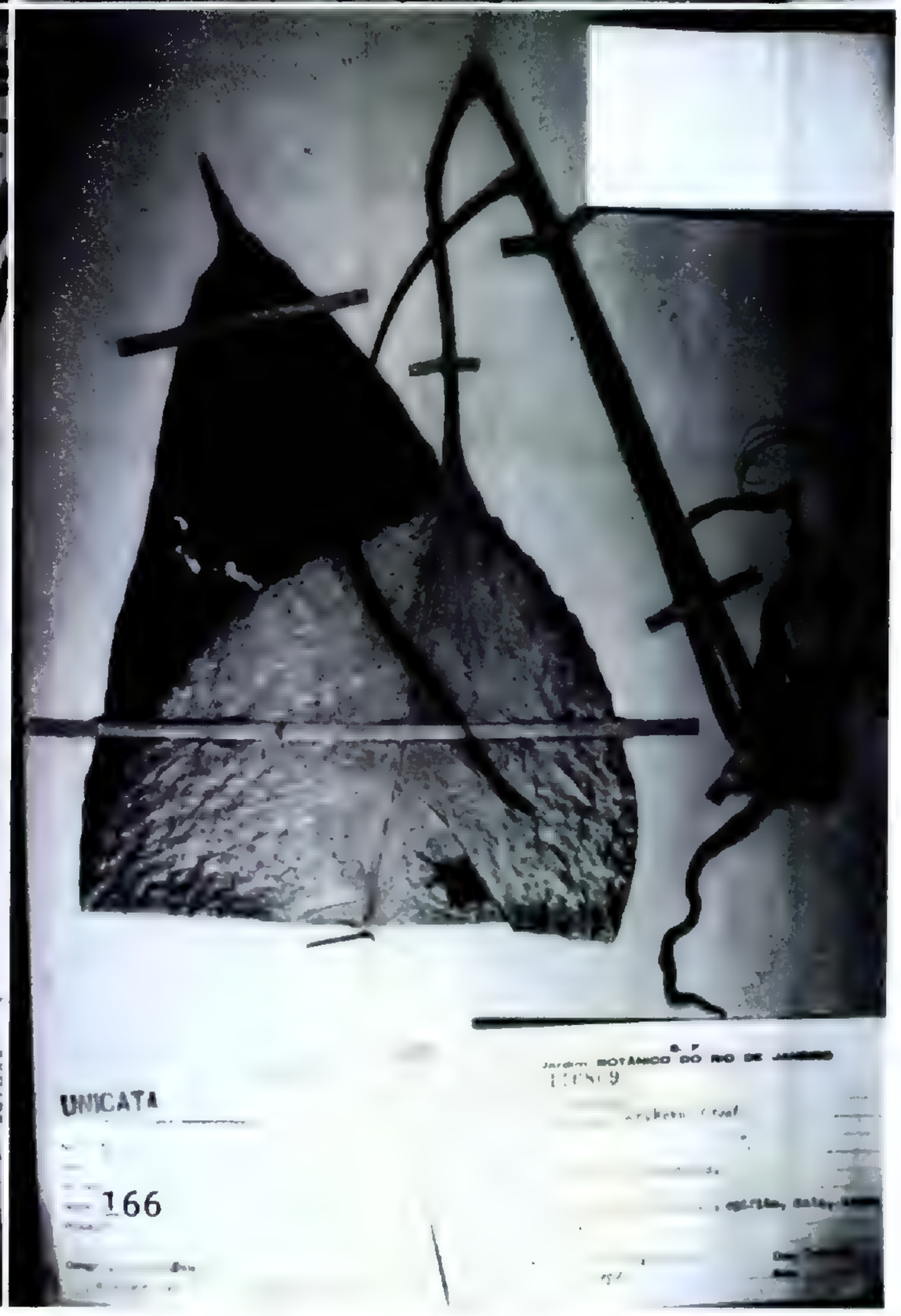
FIGURES 159–162.—159–160. *Anthurium holmnielsenii* Croat, *Croat 50689*.—161. *A. holmnielsenii* Croat, *Croat 61640*.—162. *A. jenmanii* Engl., cultivated at Port of Spain Bot. Gard.

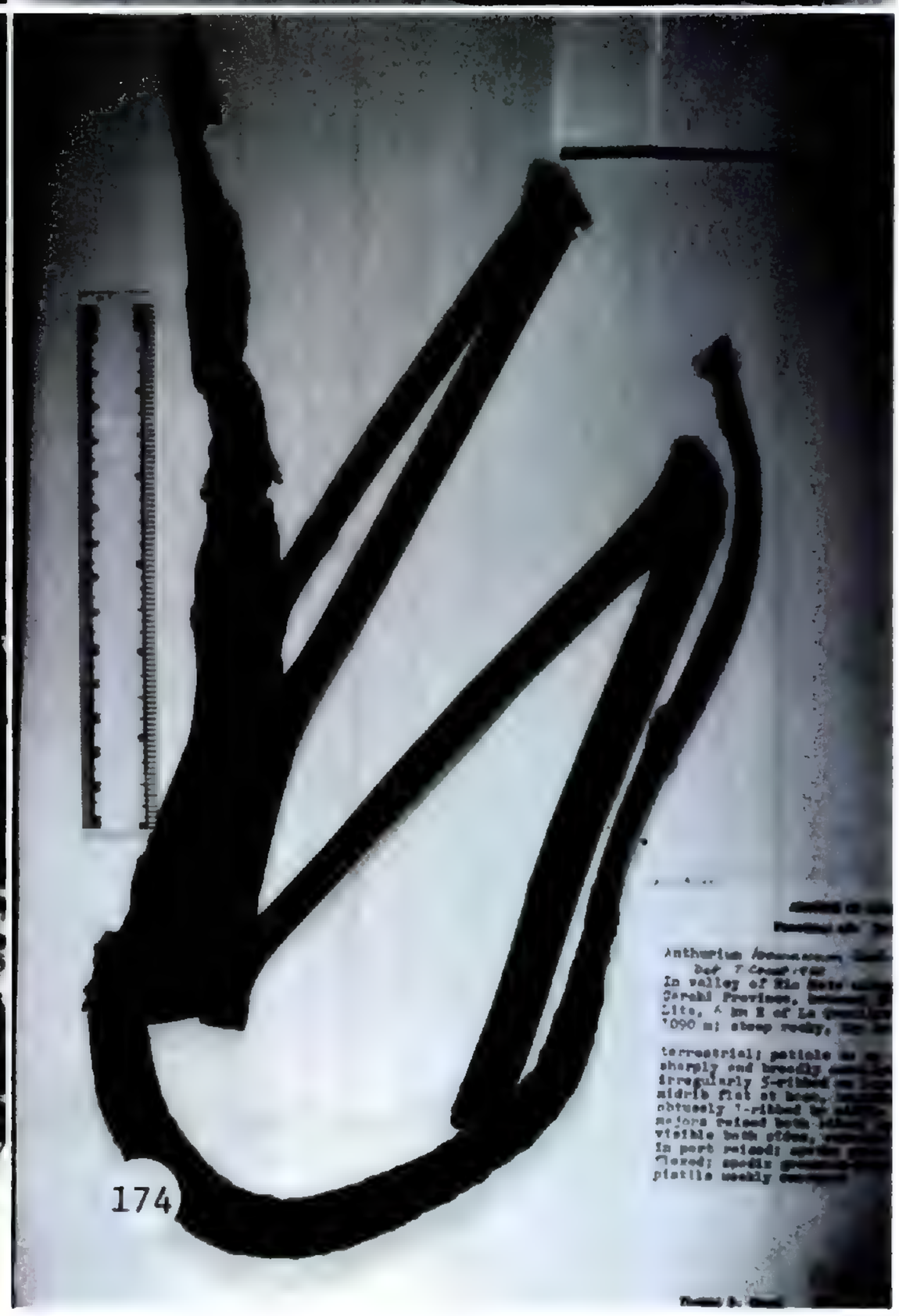






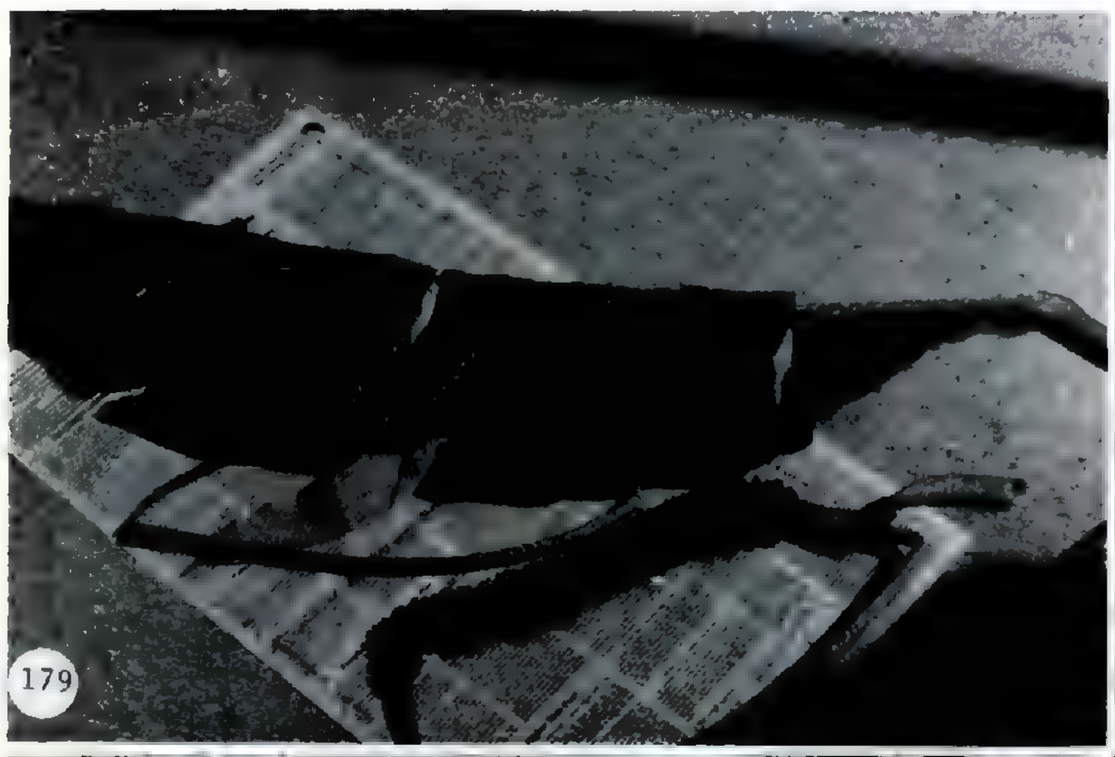
FIGURES 163–166.—163, 164. *A. johnsoniae* Croat, *Croat 62835*.—165. *A. knappiae* Croat, *Knapp et al. 8544*.—166. *A. krukovii* Croat, *Duarte 6958*.

FIGURES 167–170.—167, 168. *Anthurium latissimum* Engl., *Croat 57727.*—169. *A. latissimum* Engl., *Croat 51171.*—170. *A. latissimum* Engl., *Croat 52230.*

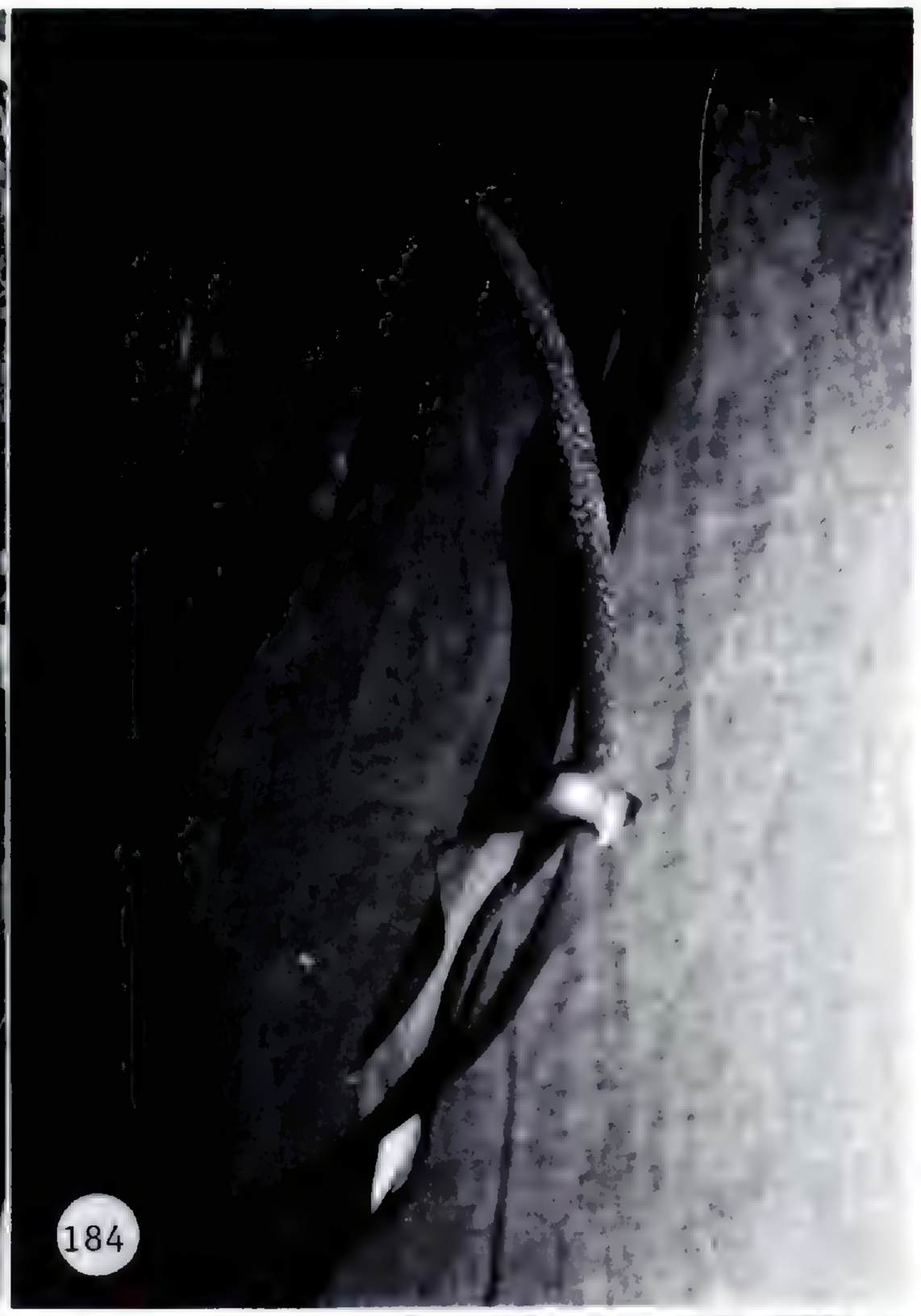


FIGURES 171–174.—171. *Anthurium lennartii* Croat, *Harling & Andersson 22159*.—172, 173. *A. leonianum* Sodiro, *Madison et al. 4960*.—174. *A. leonianum* Sodiro, *Croat 38986*.

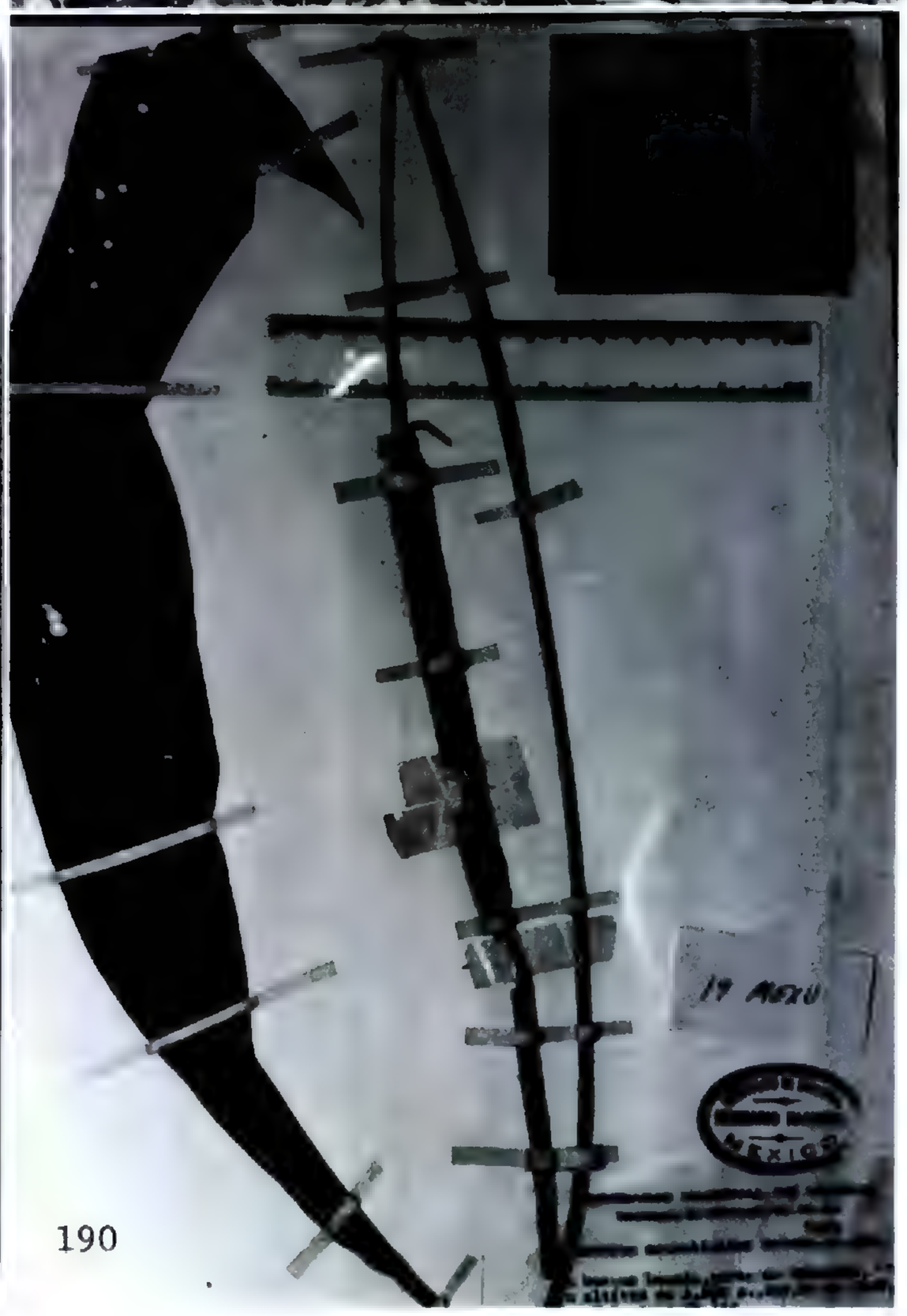
FIGURES 175-178.—175. *Anthurium lindmanianum* Engl., cultivated at Munich Bot. Gard.—176. *A. lindmanianum* Engl., cultivated by Burle-Marx.—177. *A. lindmanianum* Engl., *Croat 57157*, cultivated at Tropic World, San Diego, California.—178. *A. linguifolium* Engl., *Croat 50697*.



FIGURES 179–182.—179. *Anthurium johnsoniae* Croat, *Croat 62835*.—180. *A. linguifolium* Engl., *Croat 50697*.—181. *A. llewelynii* Croat, *Croat 51092*.—182. *A. loretense* Croat, *Croat 51225*.



FIGURES 183–186.—183, 184. *Anthurium llewelynii* Croat, *Croat 51092*.—185. *A. llewelynii* Croat, *Croat 57212*.—186. *A. loretense* Croat, *Croat 51225*.



FIGURES 187–190.—187. *Anthurium luteynii* Croat, *Croat 49071.*—188. *A. luteynii* Croat, *Croat 27169.*—189. *A. luteynii* Croat, *Croat 25521.*—190. *A. machetioides* Matuda, *Ramirez 144.*

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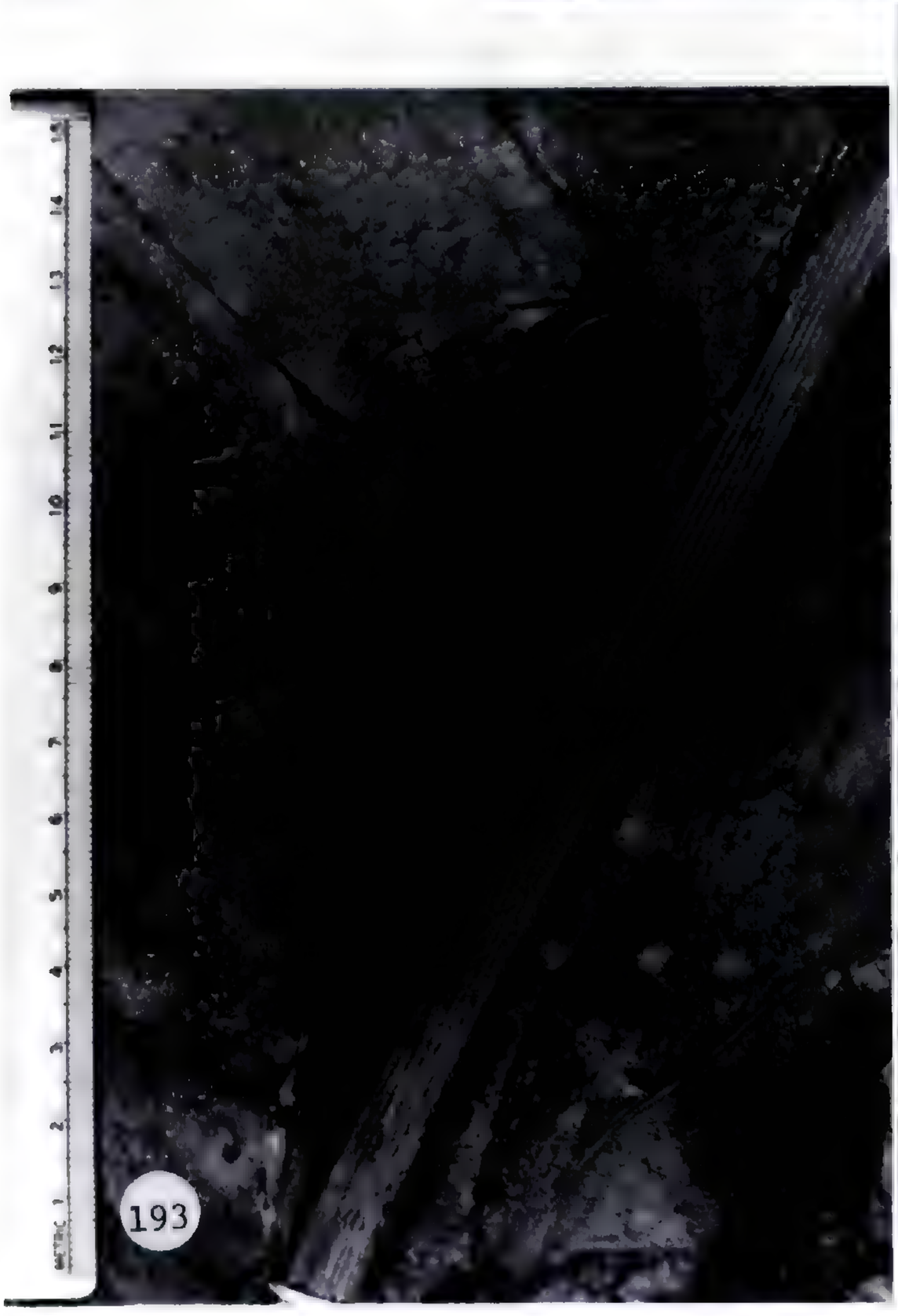

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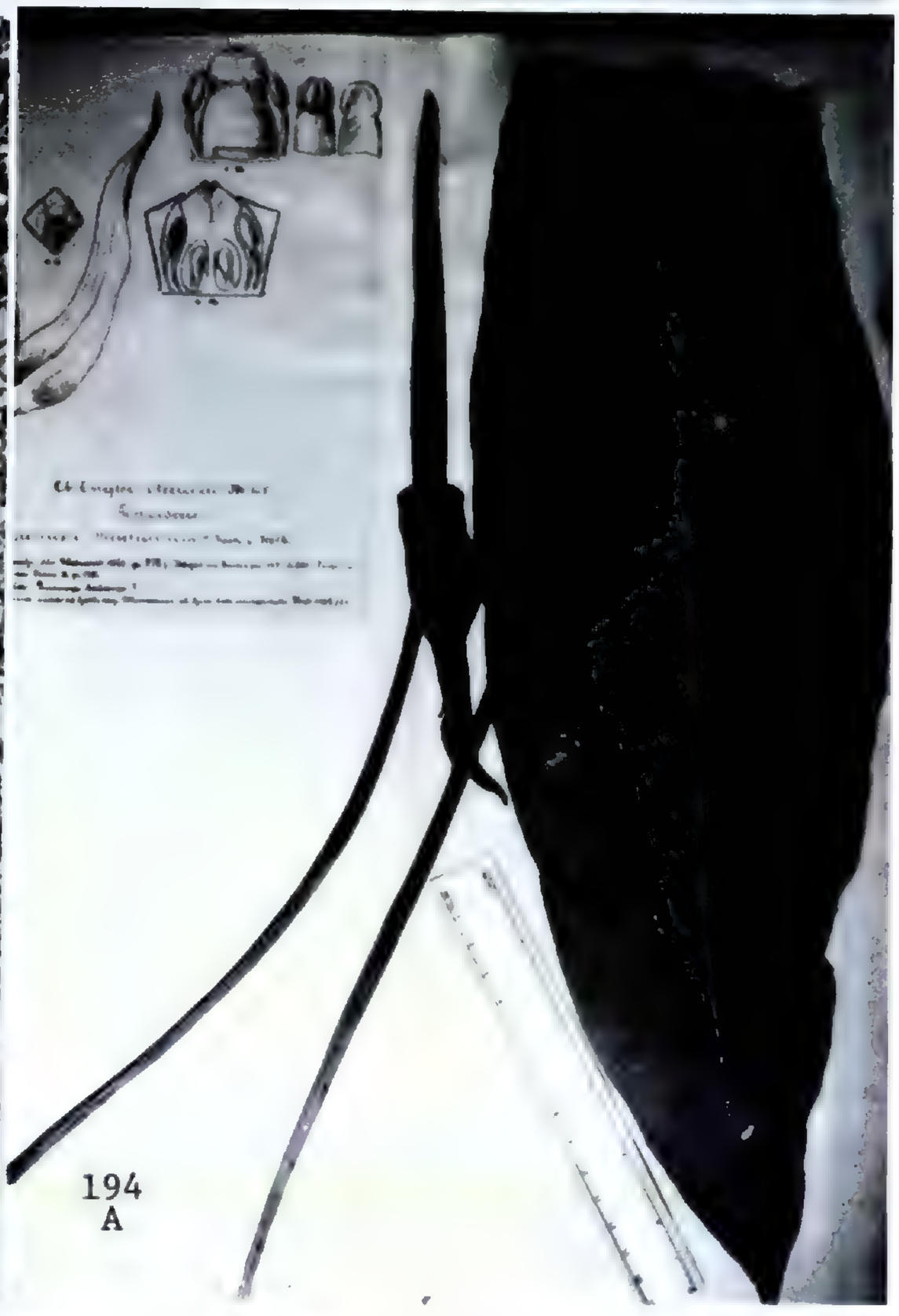
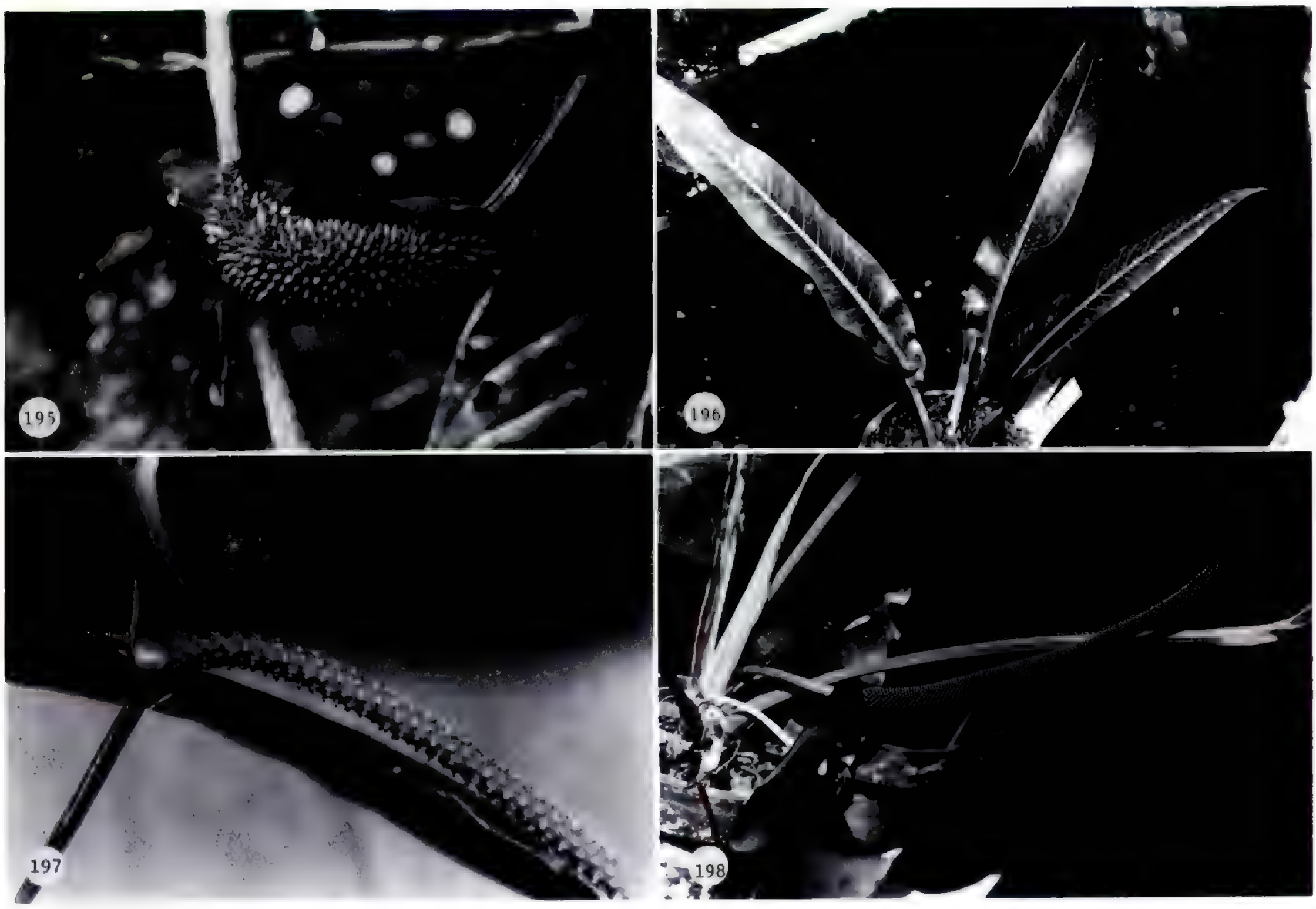
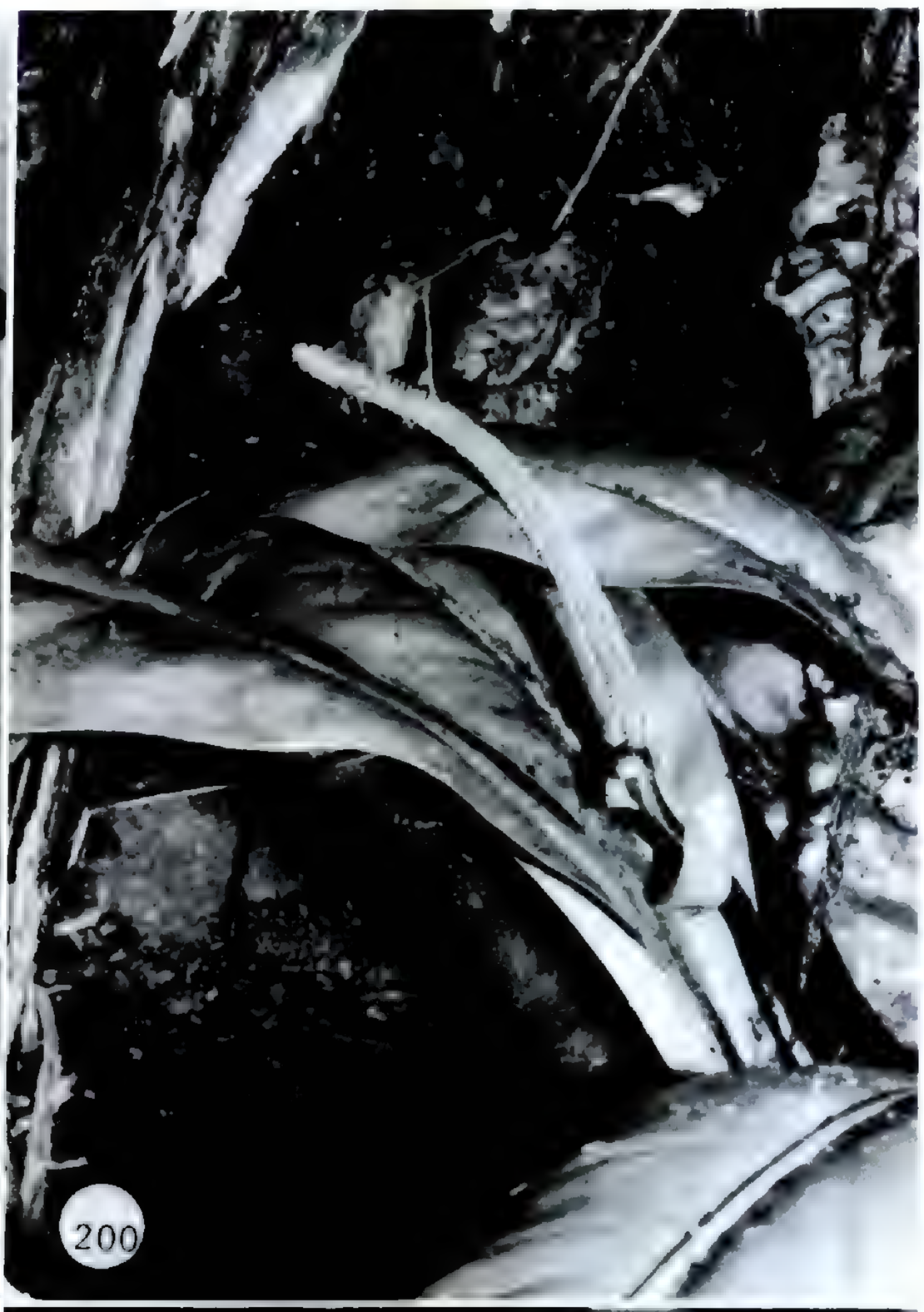
FIGURES 191–194.—191, 192. *Anthurium manabianum* Croat, *Harling & Andersson 24750.*—193. *A. galactospadix* Croat, *Prance et al. 2924.*—194. *A. martianum* K. Koch & Kolb, cultivated at Munich Bot. Gard.



FIGURES 191A–194A.—191A. *Anthurium maguirei* A. Hawkes, *LBB 16571*.—192A. *A. manuanum* Croat, *Vargas 17747*.—193A. *A. selloum* K. Koch, St. Johns, Virgin Is., cultivated by Conrad Fleming.—194A. *A. martianum* K. Koch & Kolb, cultivated at Munich Botanical Garden.

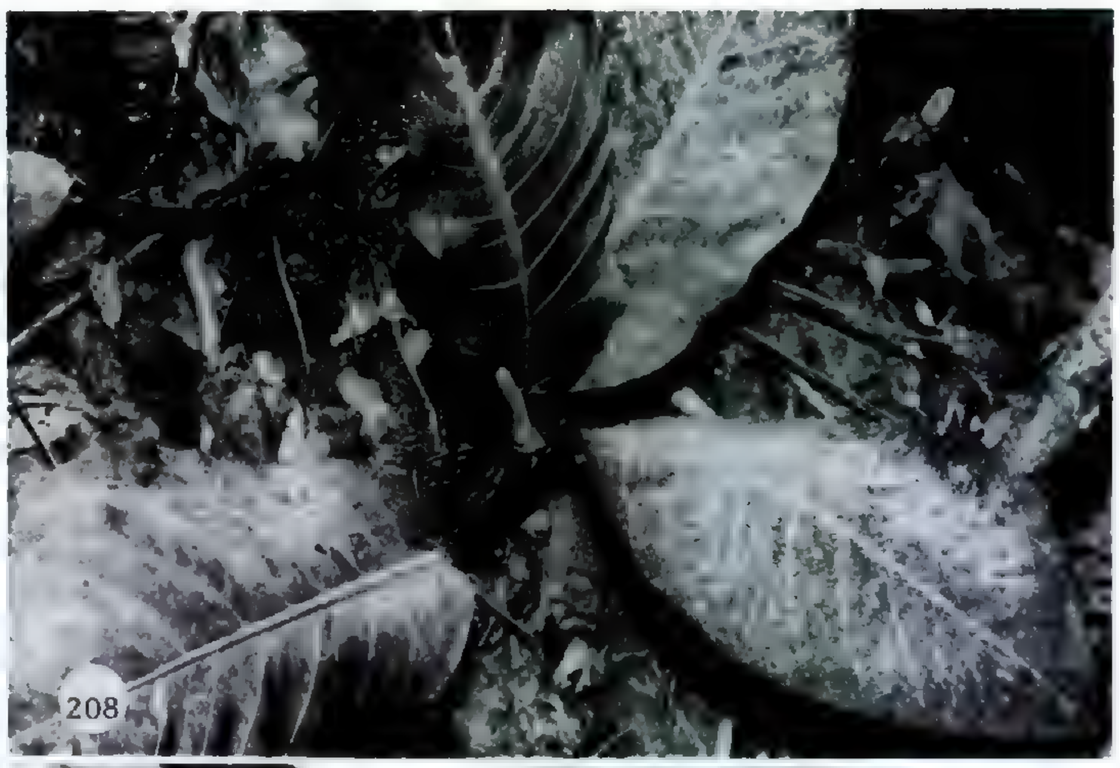


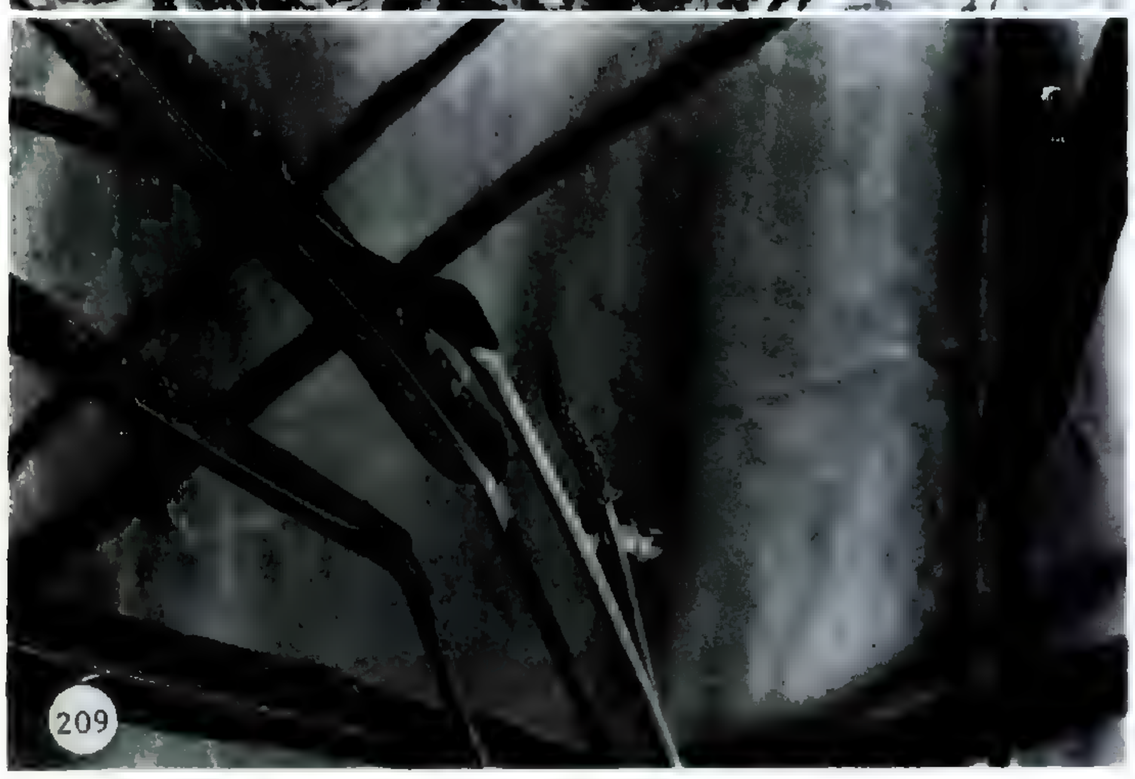
FIGURES 195–198.—195. *Anthurium luteynii* Croat, *Croat 27156*.—196. *A. martianum* K. Koch & Kolb, cultivated at Munich Bot. Gard.—197. *A. napaeum* Engl., *Croat 55782*.—198. *A. nervatum* Croat, *Croat 27329*.



FIGURES 199–202.—199. *Anthurium napaeum* Engl., *Croat 57035*.—200. *A. napaeum* Engl., *Croat 50876*.—201. *A. narinoense* Croat, *Gentry et al. 55343*.—202. *A. nervatum* Croat, *Croat 48912*.

FIGURES 203–206.—203, 204. *Anthurium obscurinervium* Croat, *Croat 50914*.—205. *A. oerstedianum* Schott, *Croat 43419*.—206. *A. oerstedianum* Schott, *Croat 35293*.





FIGURES 207–210.—207, 208. *Anthurium nizandense* Matuda, *Croat 45756*.—209, 210. *A. ottonis* K. Krause, *Solomon 8652*.

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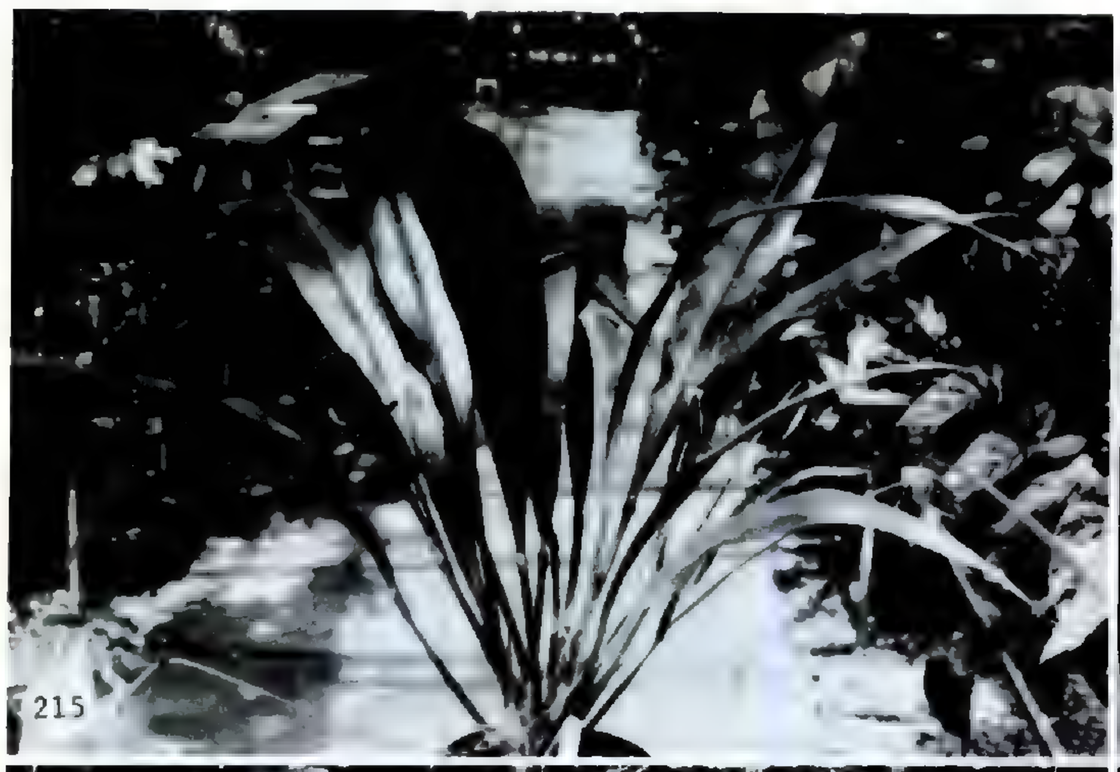

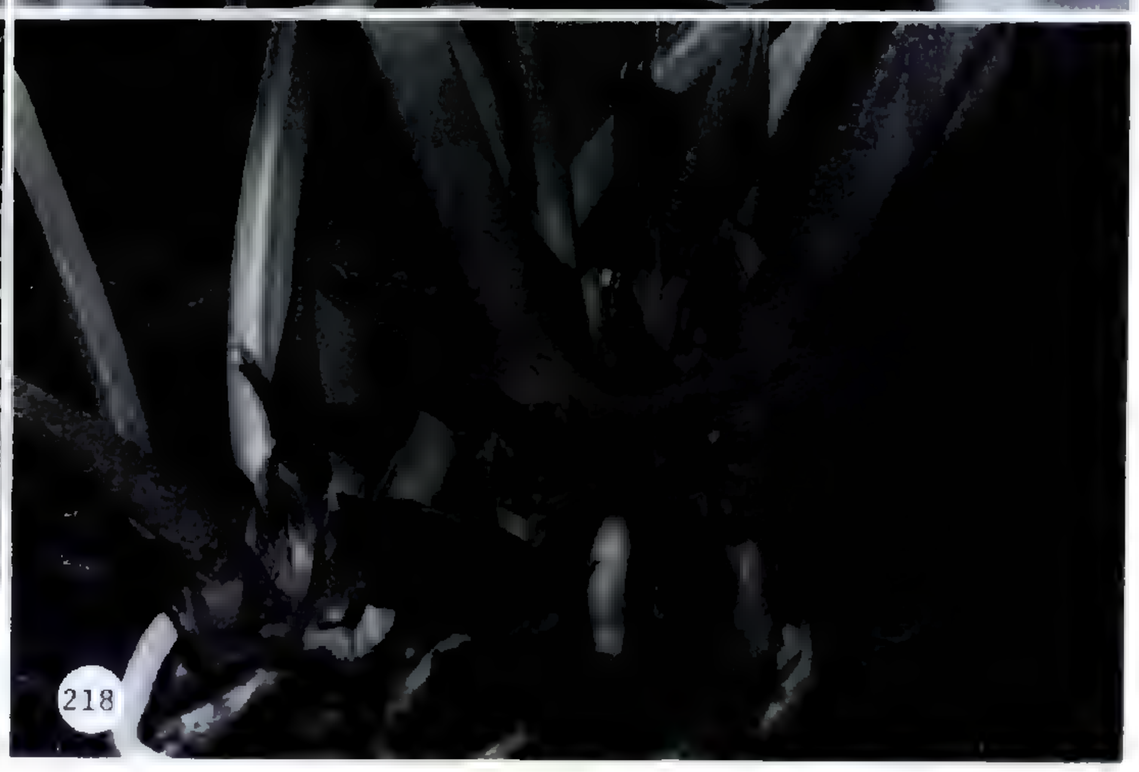

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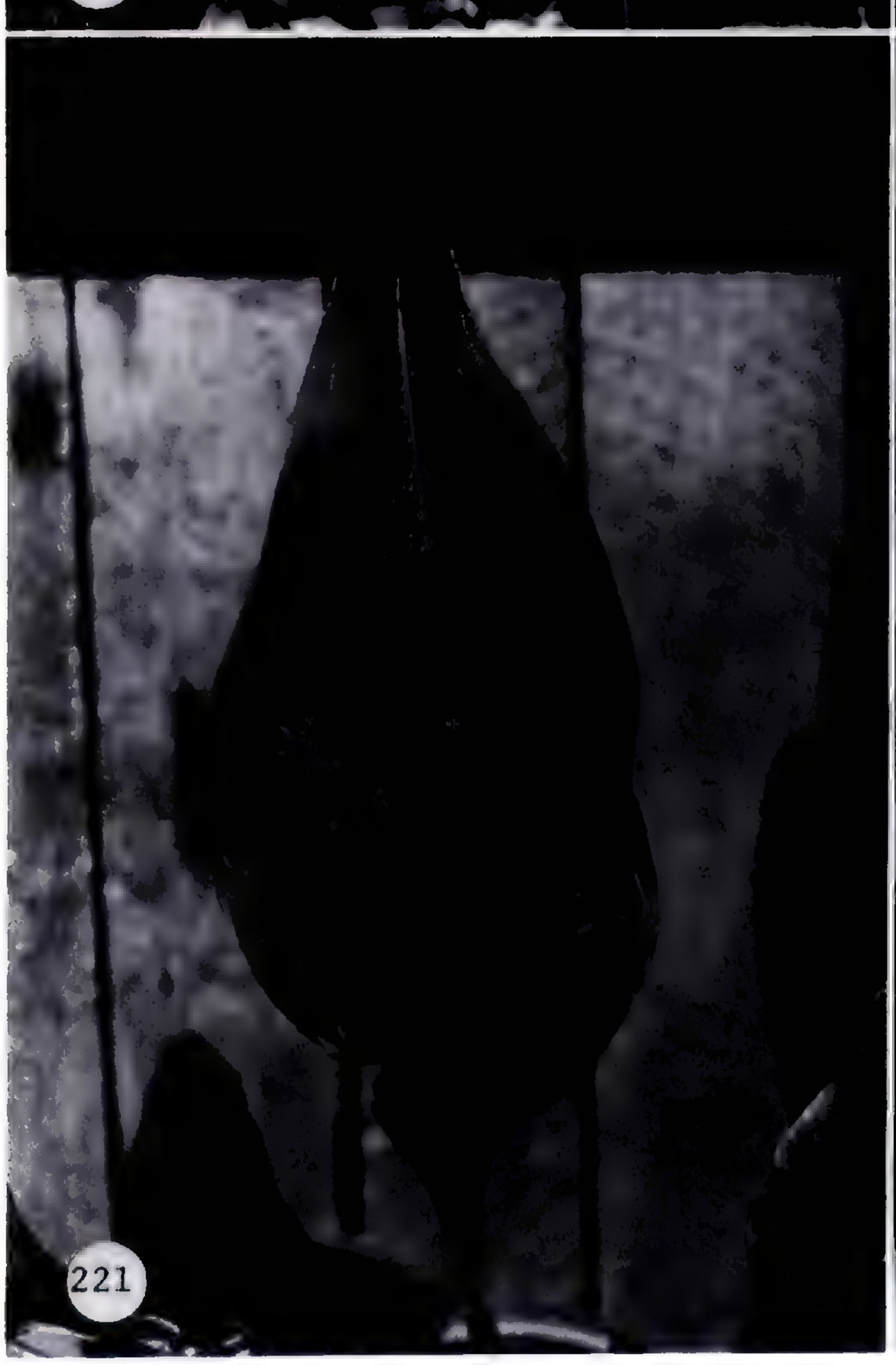
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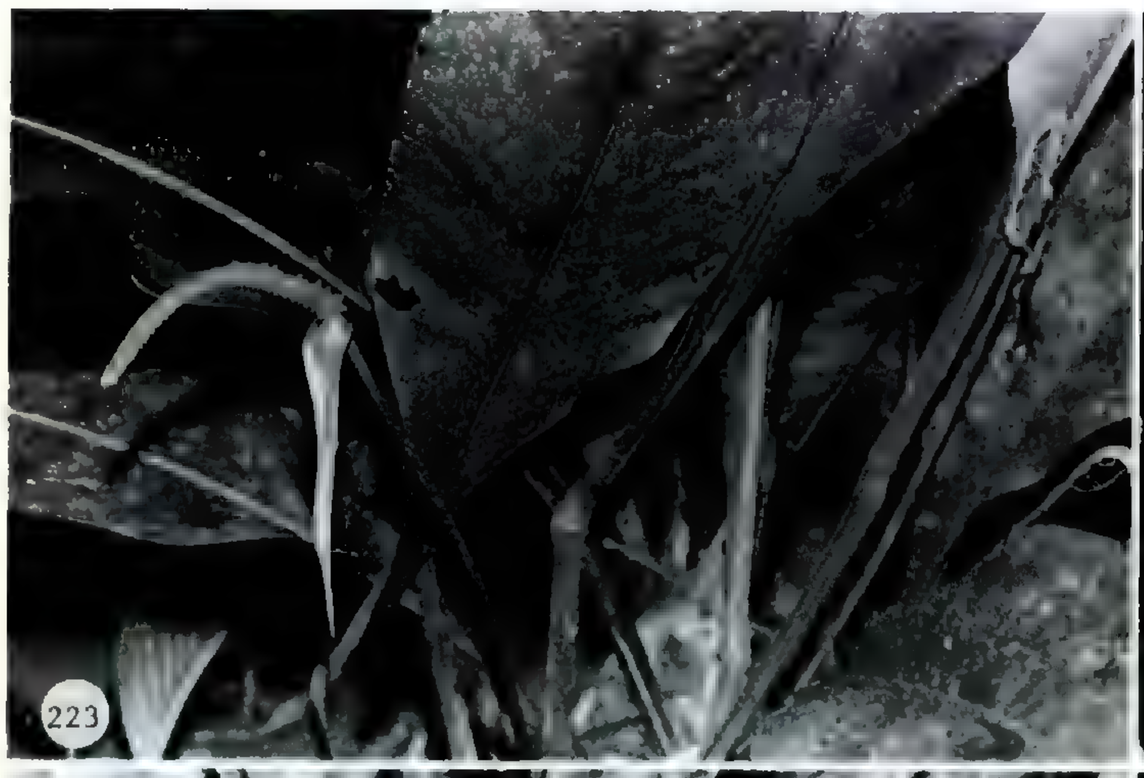

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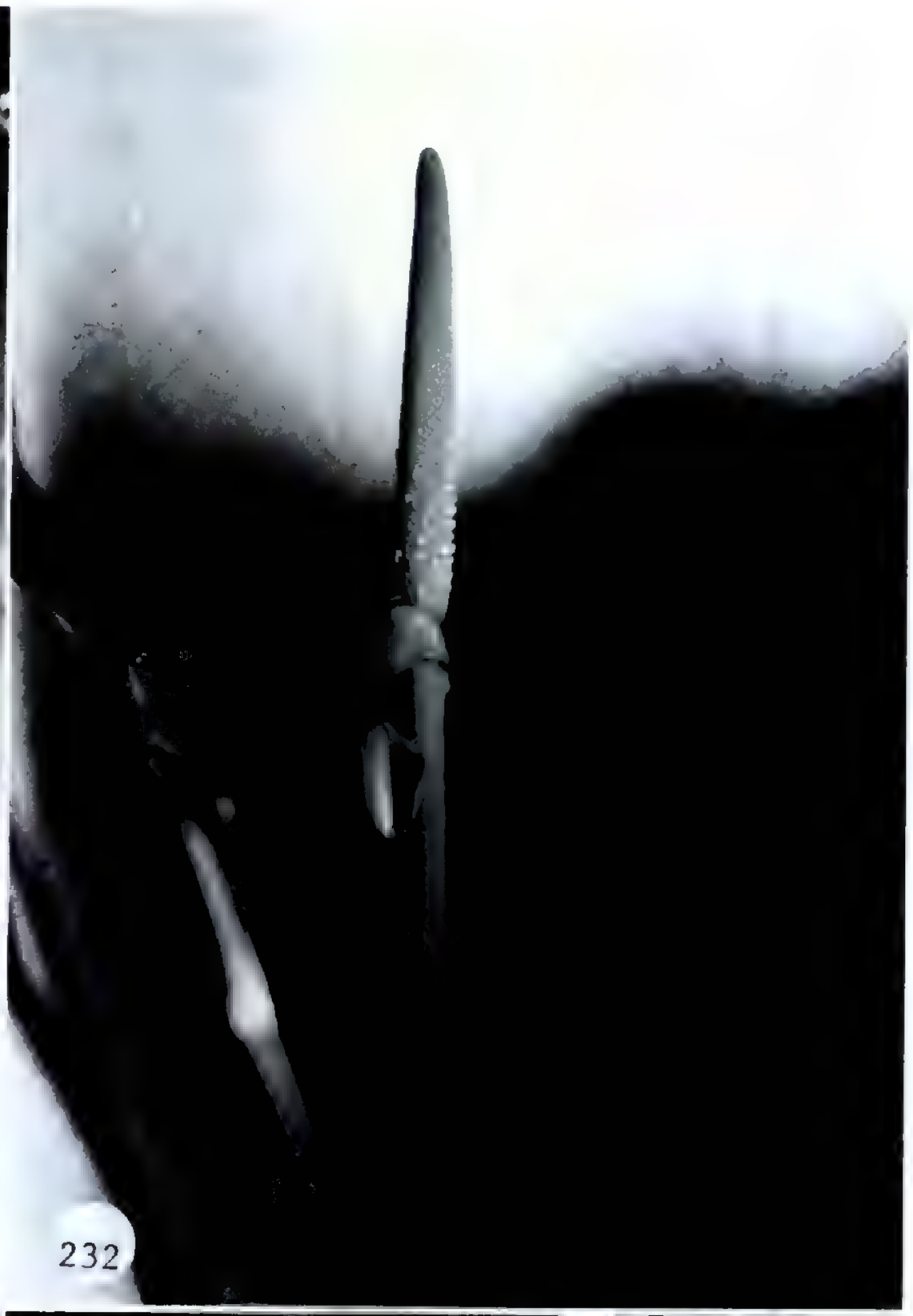

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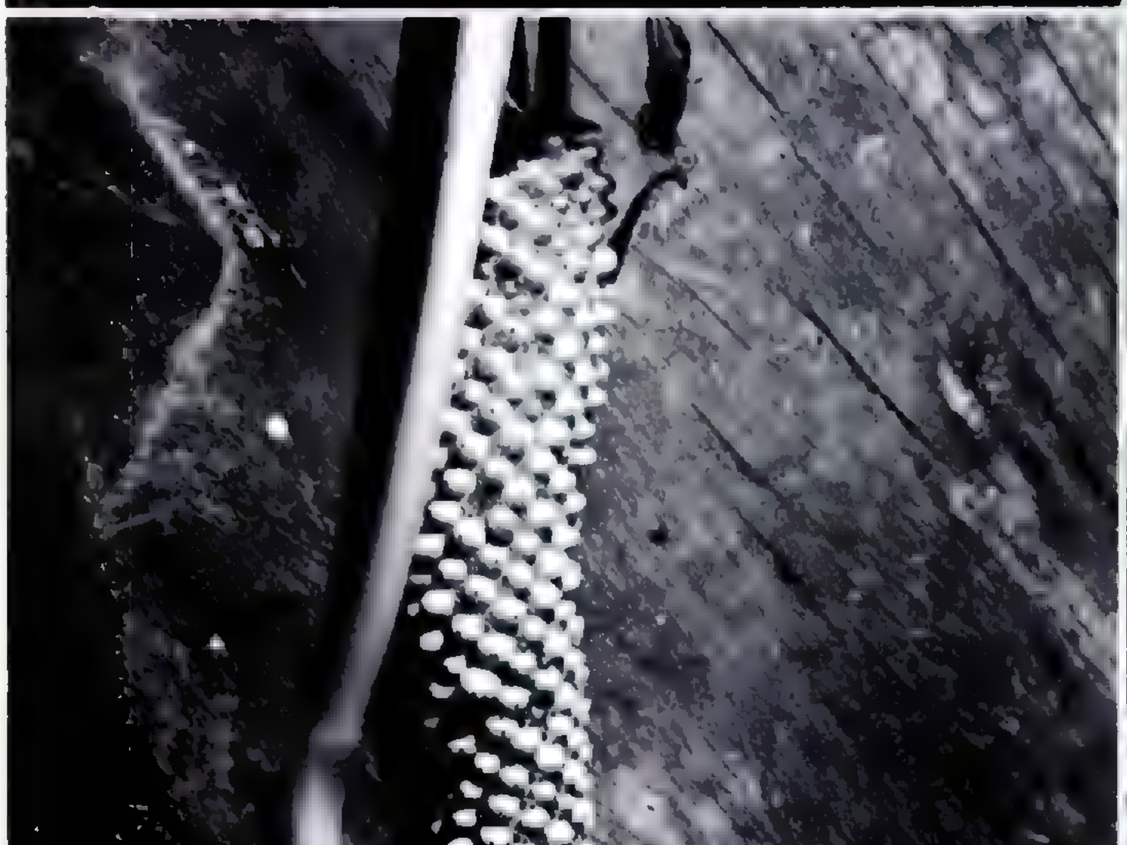

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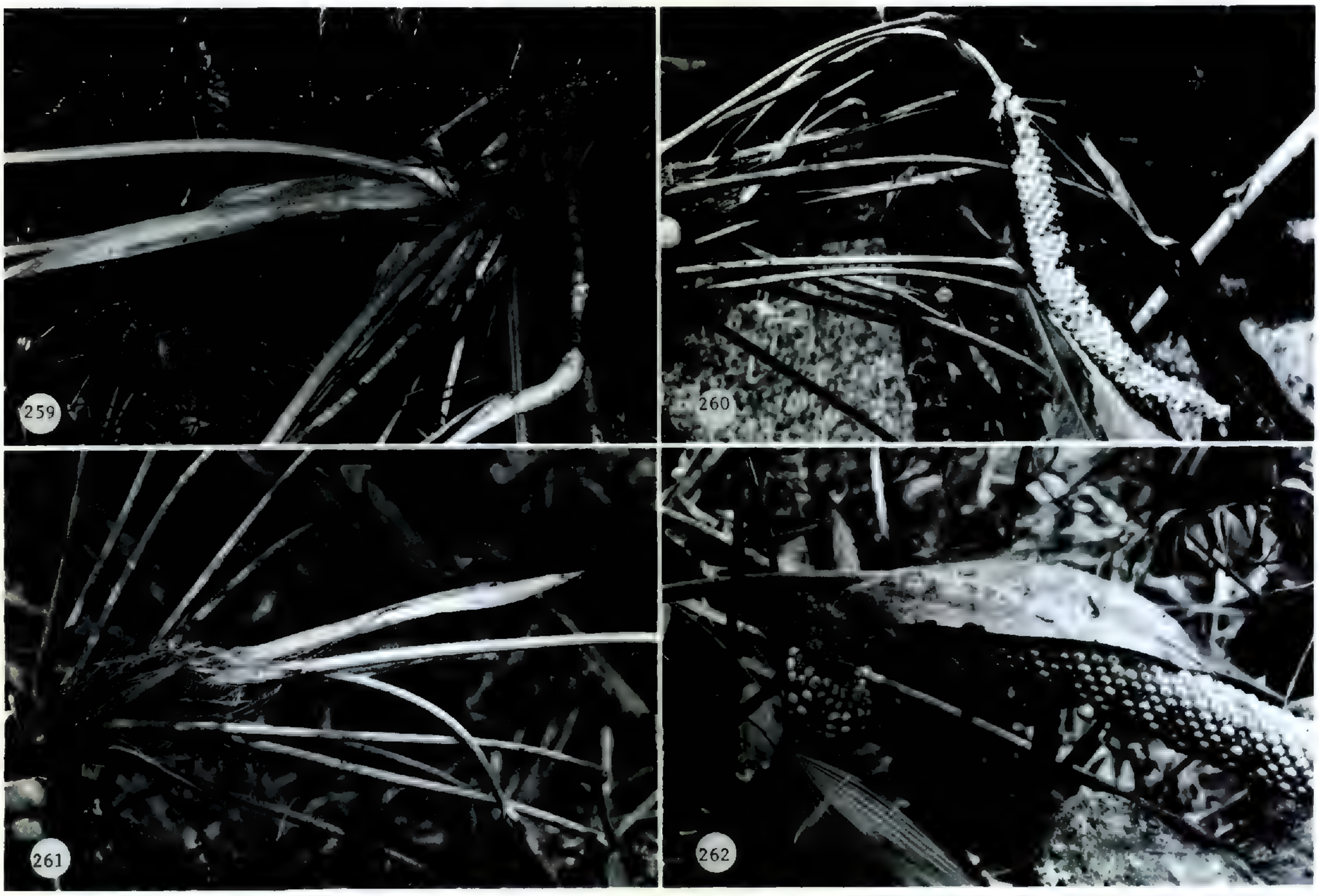

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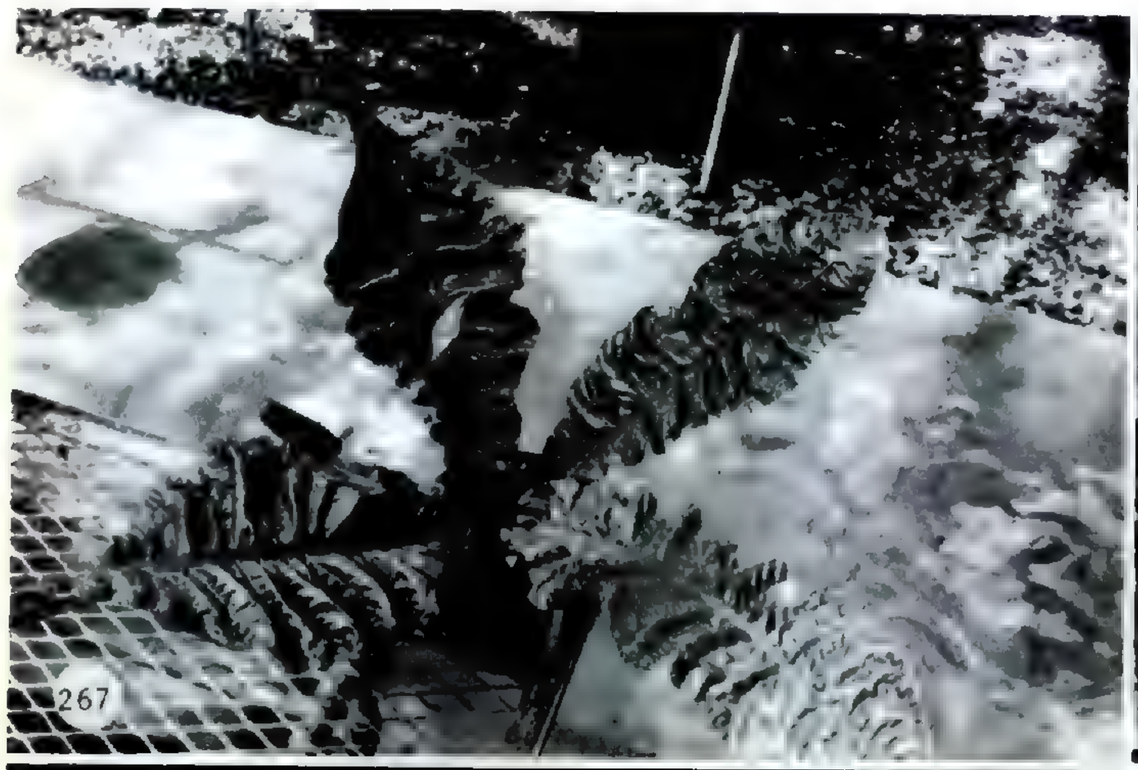

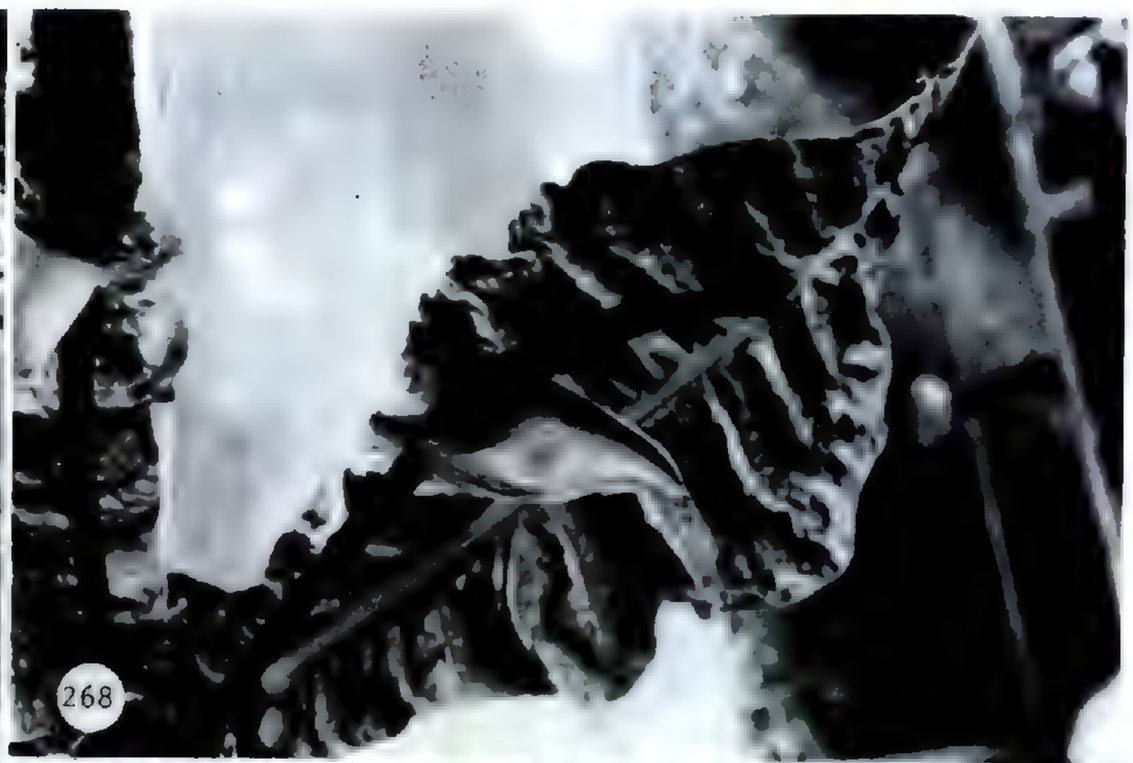

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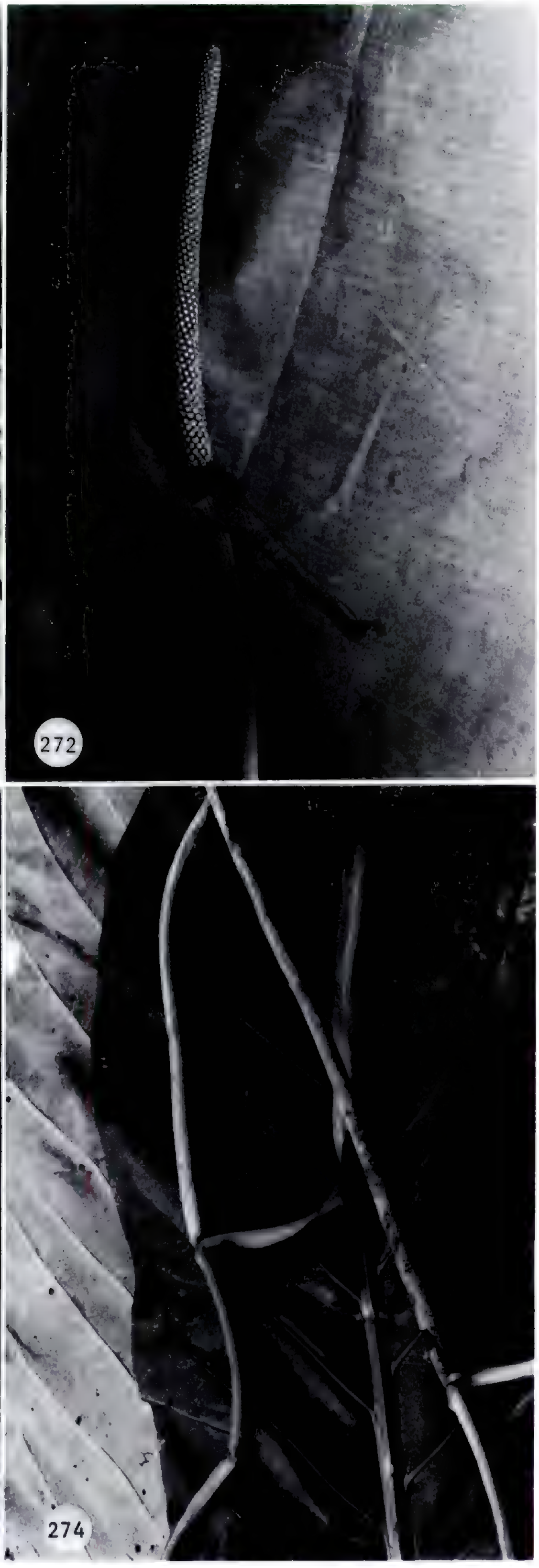

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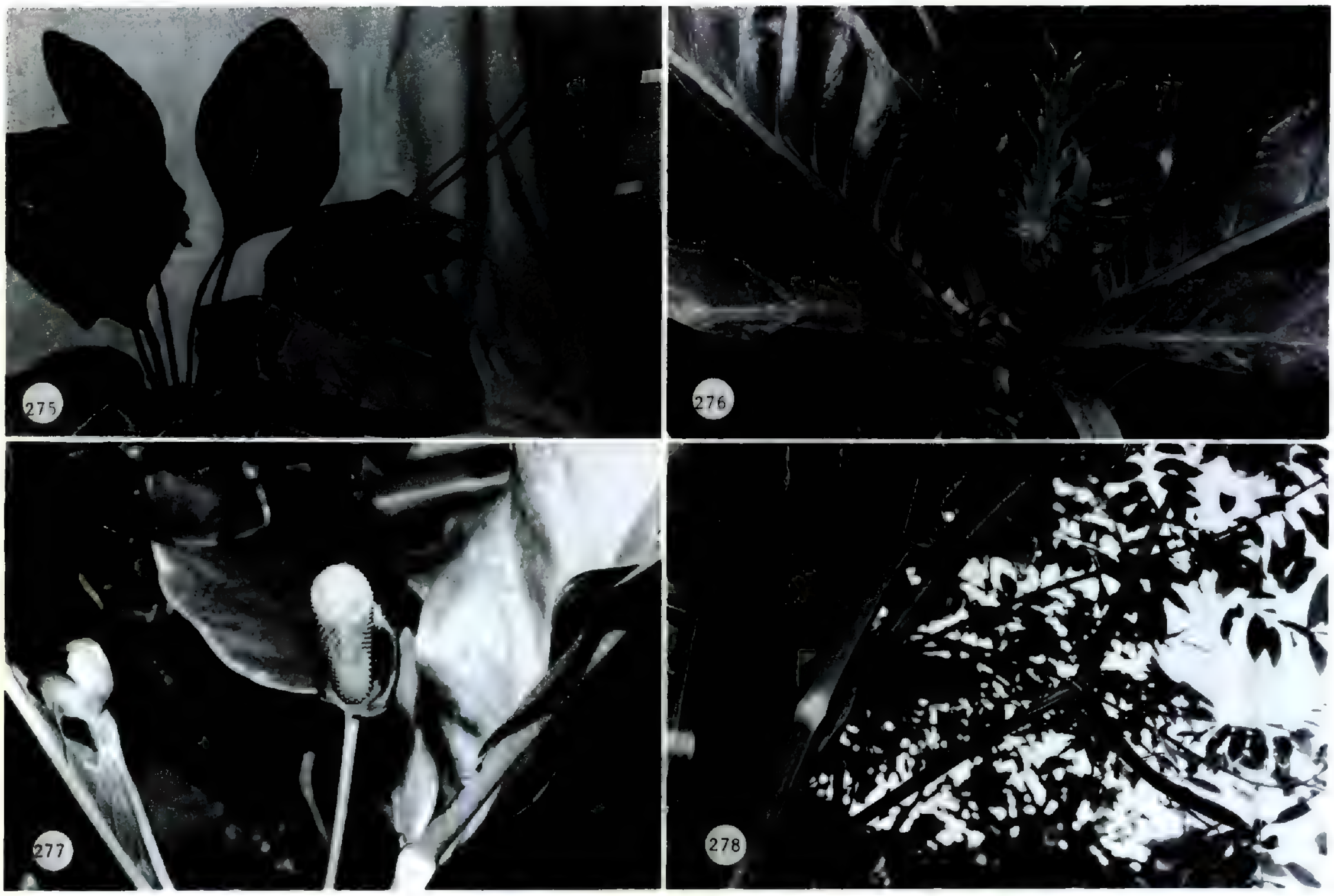

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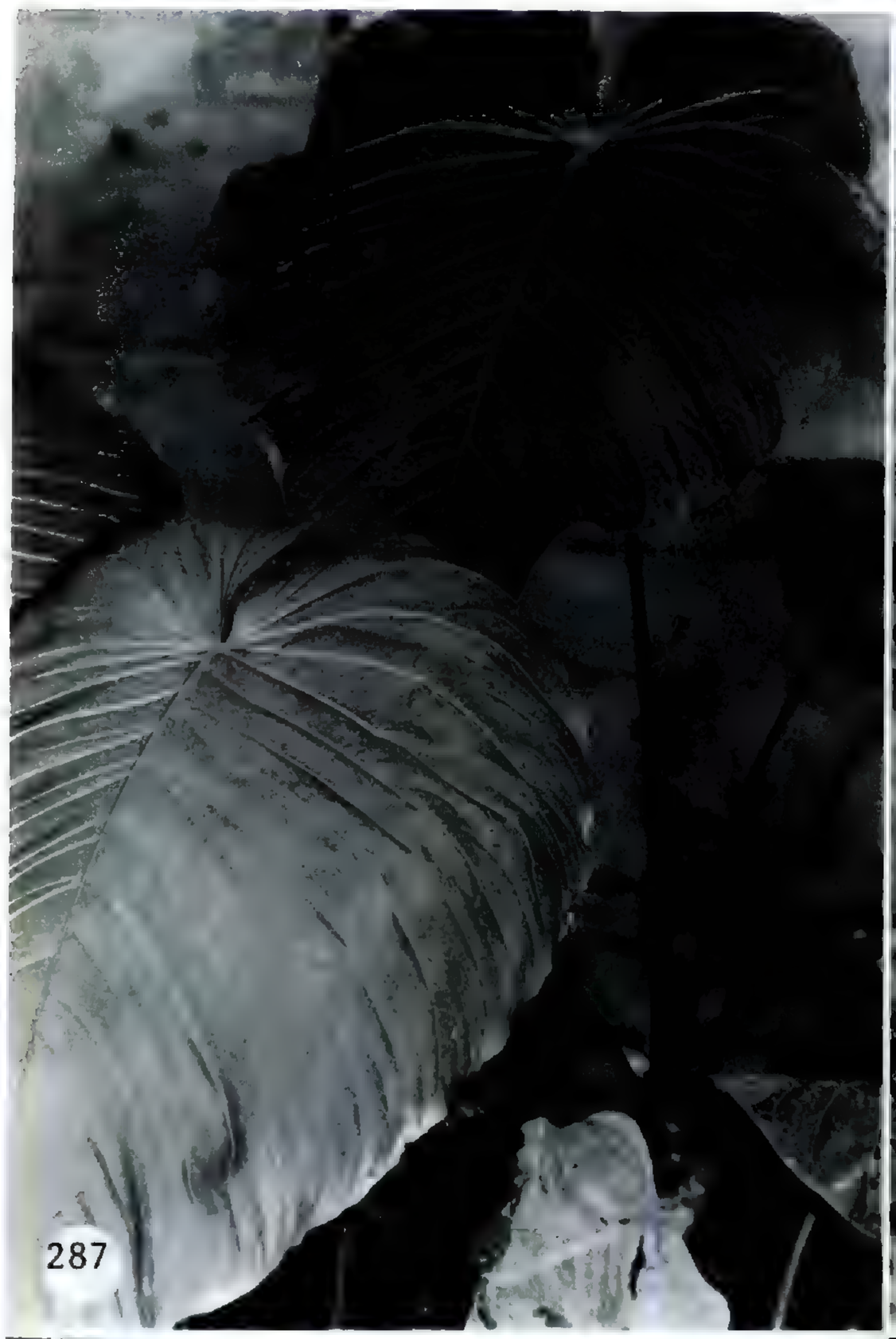

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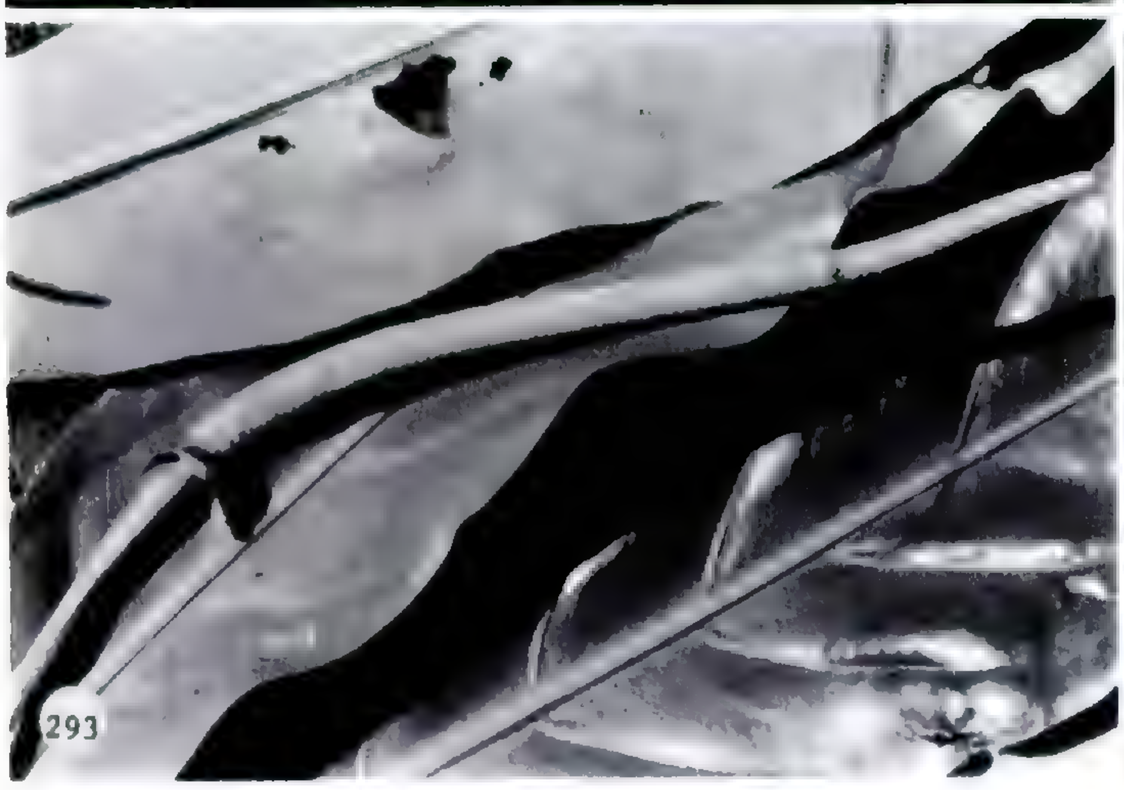

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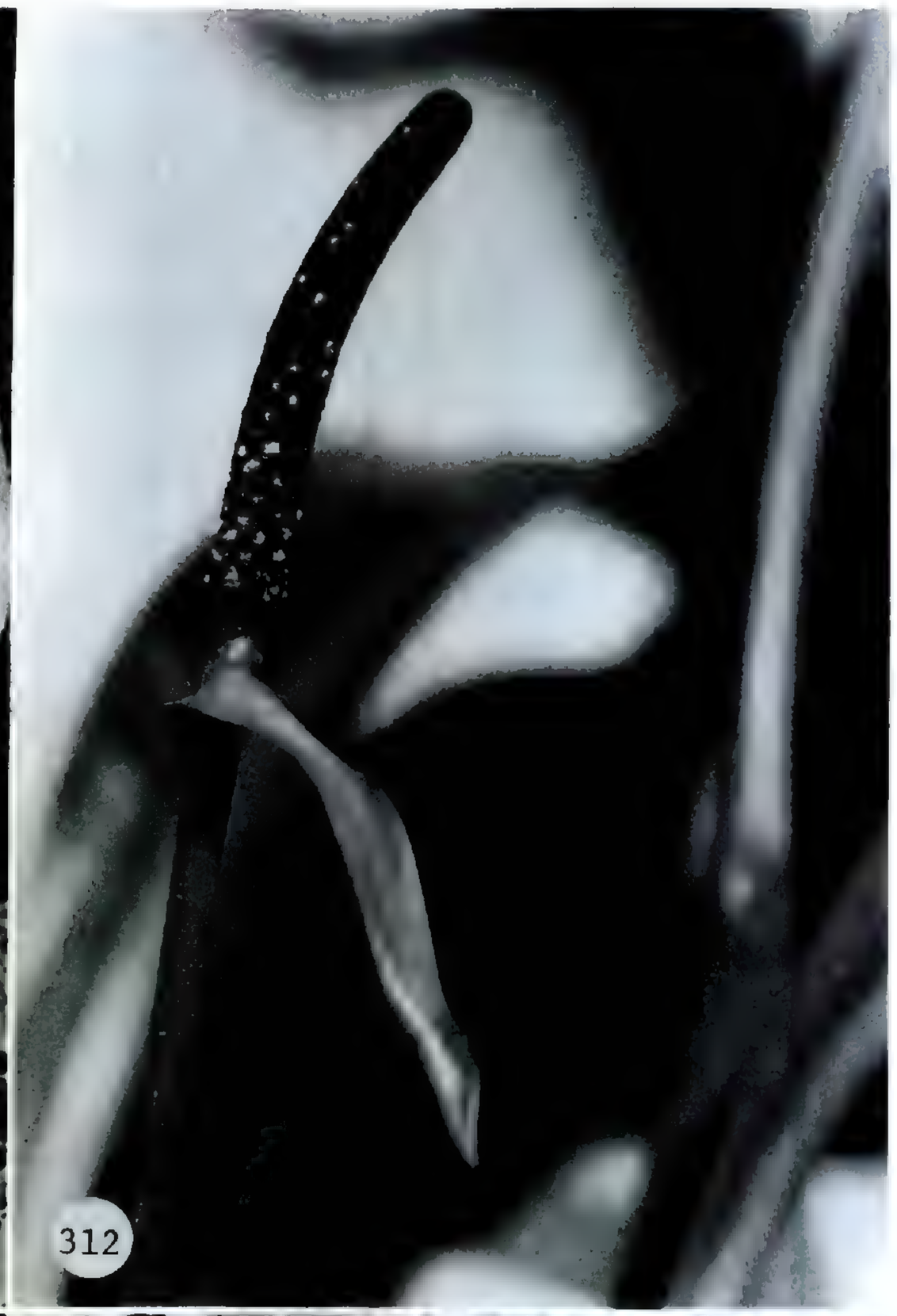

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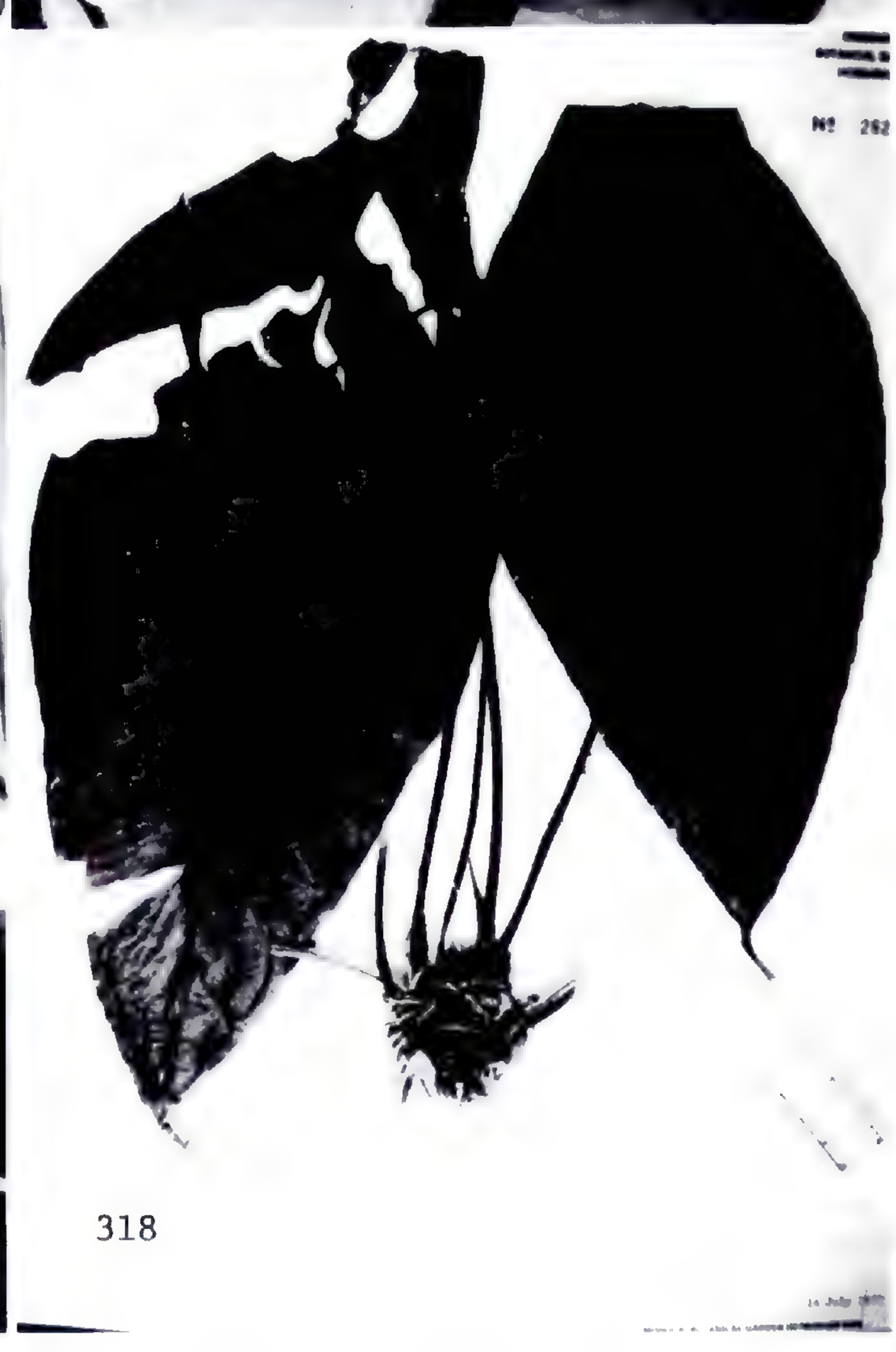

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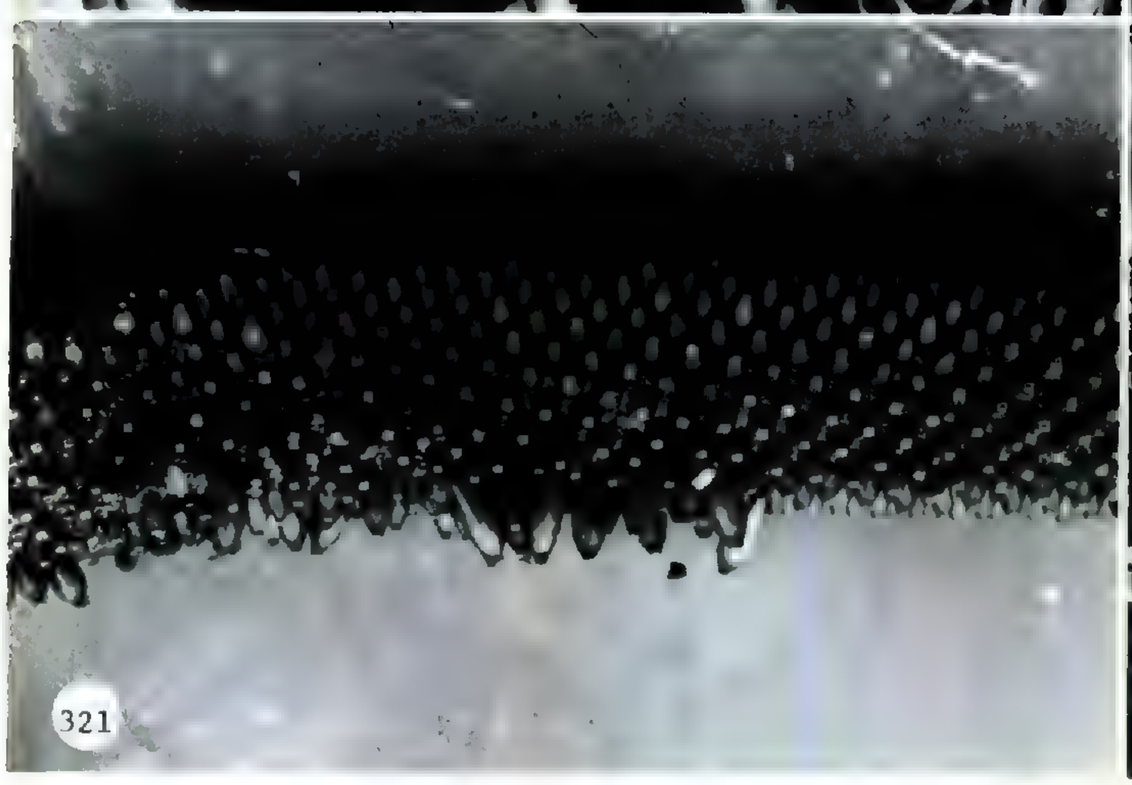

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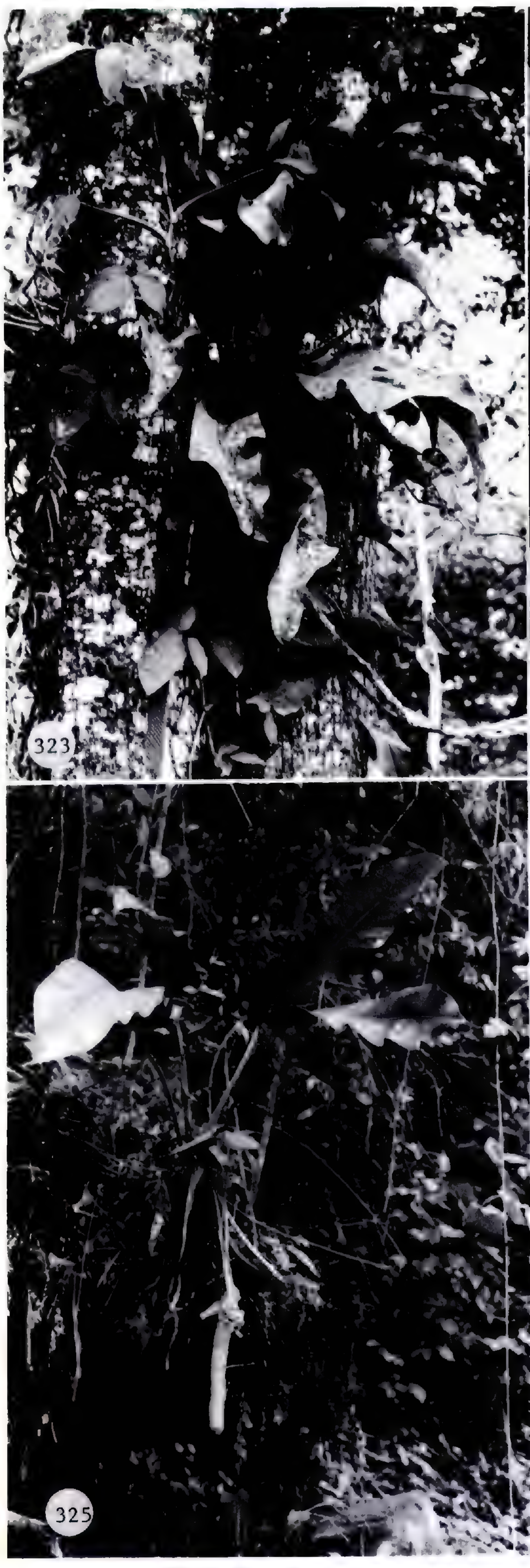

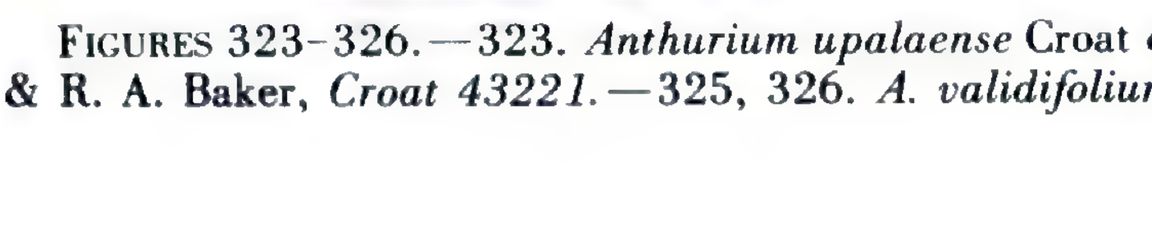

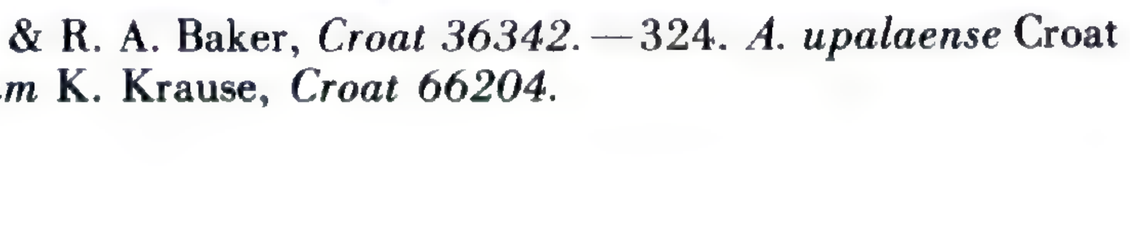

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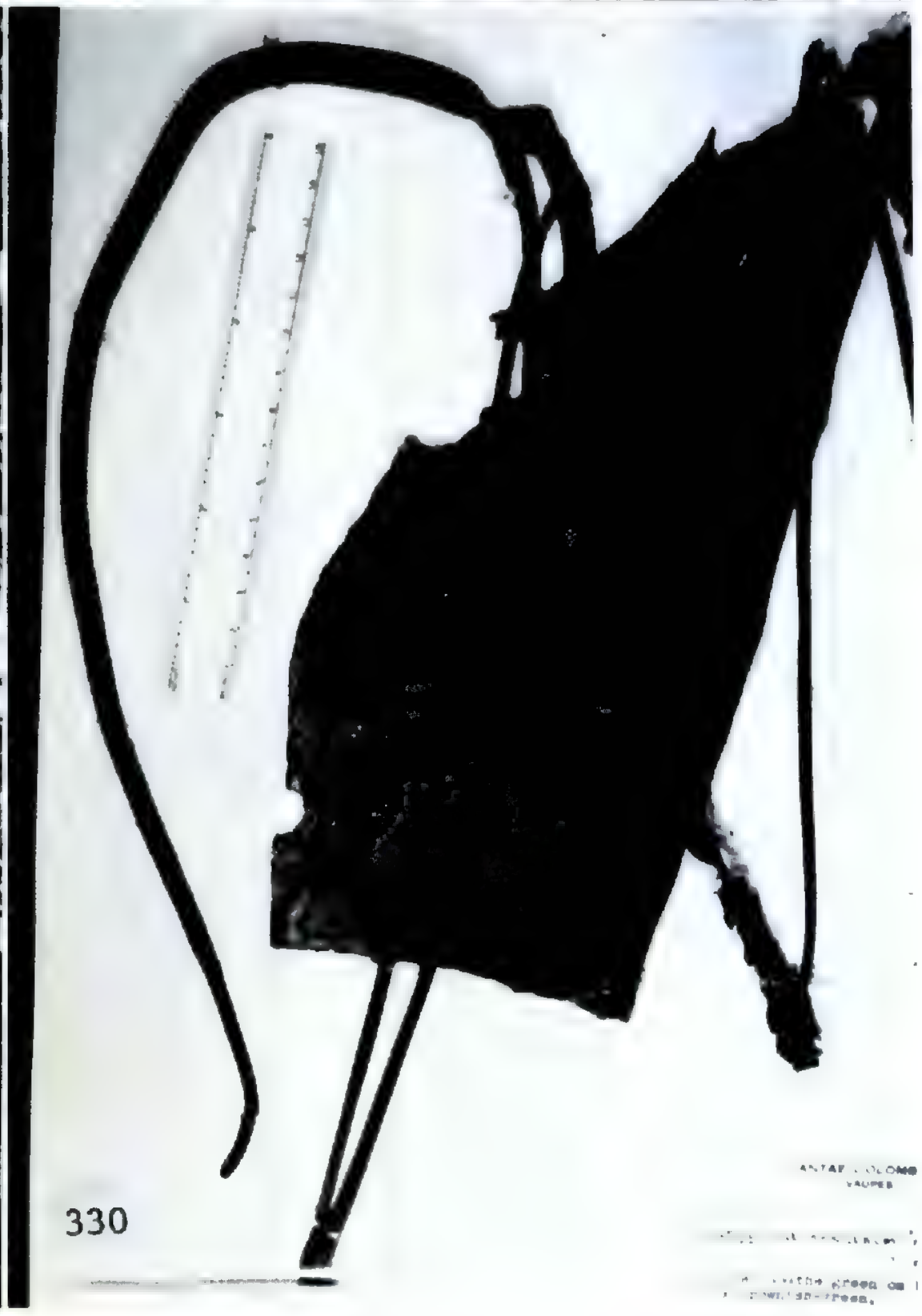

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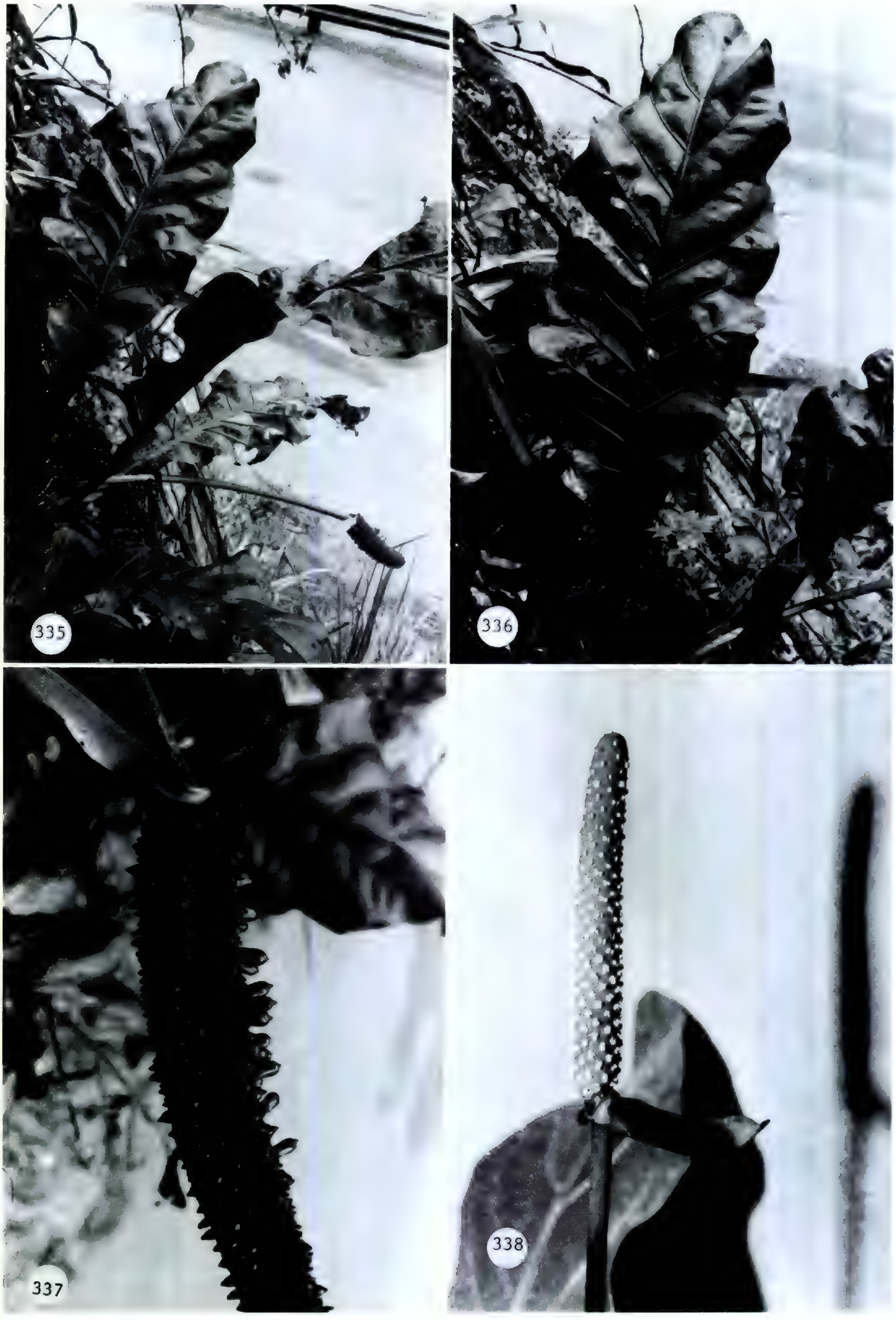

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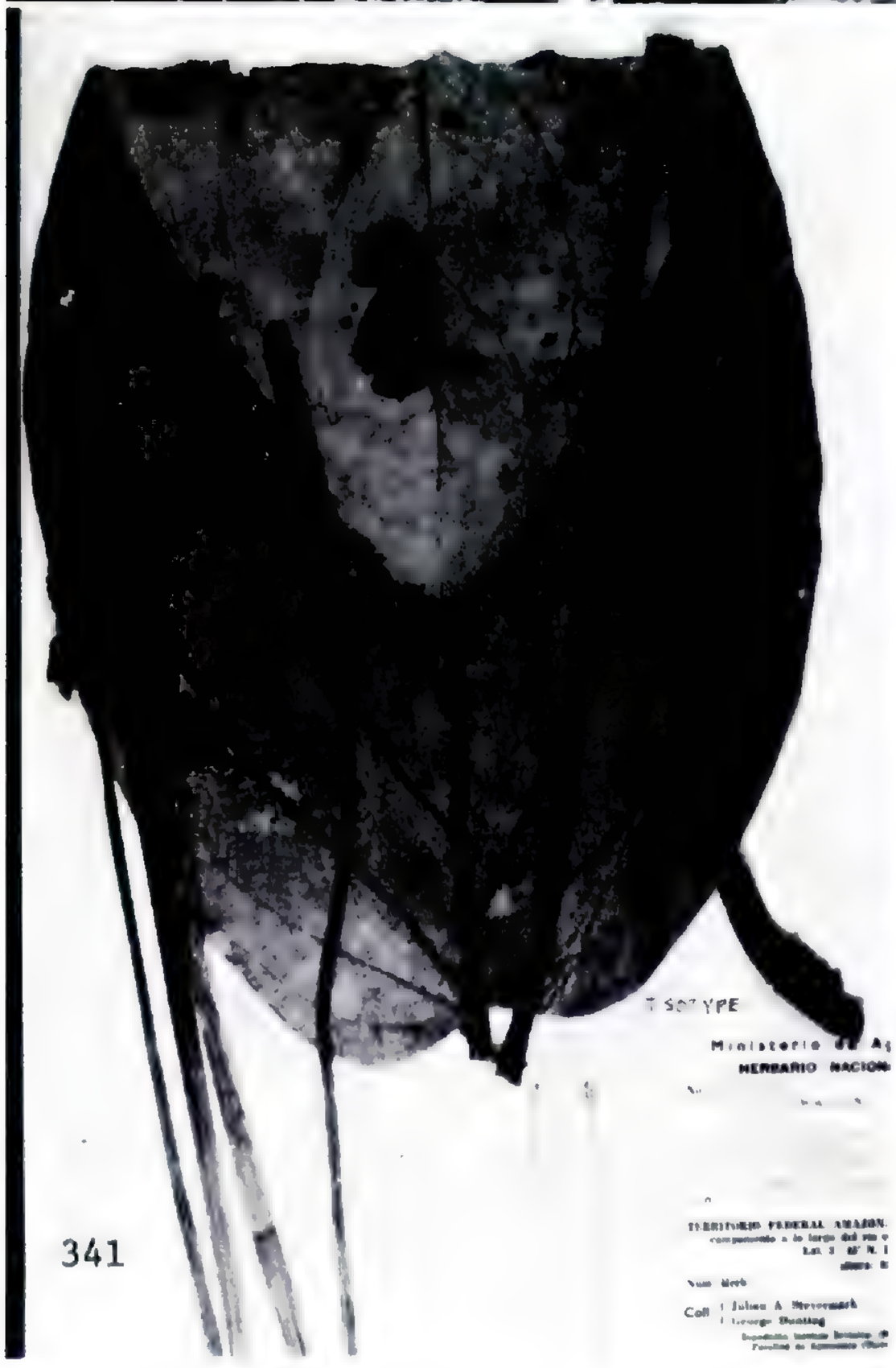

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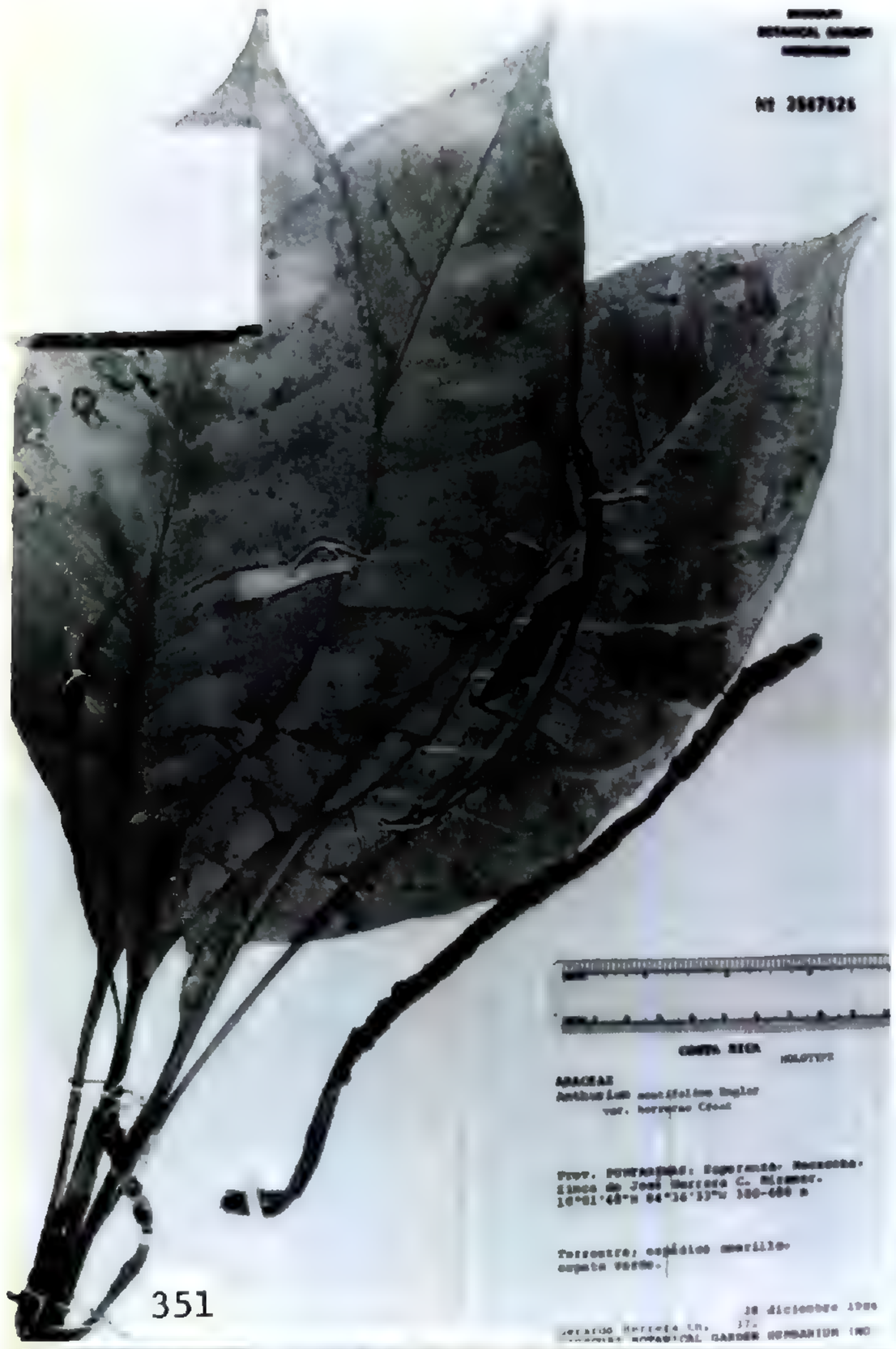

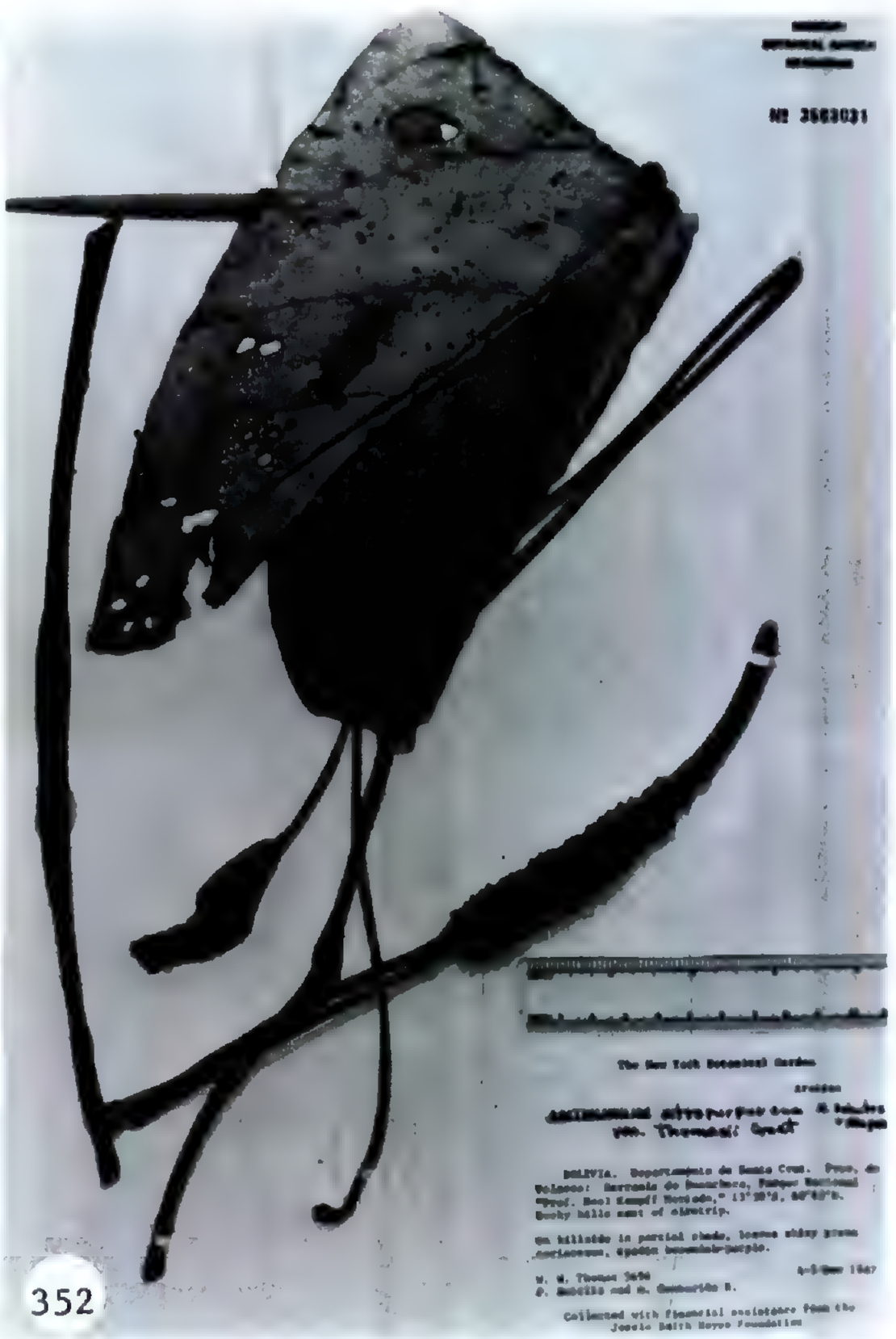

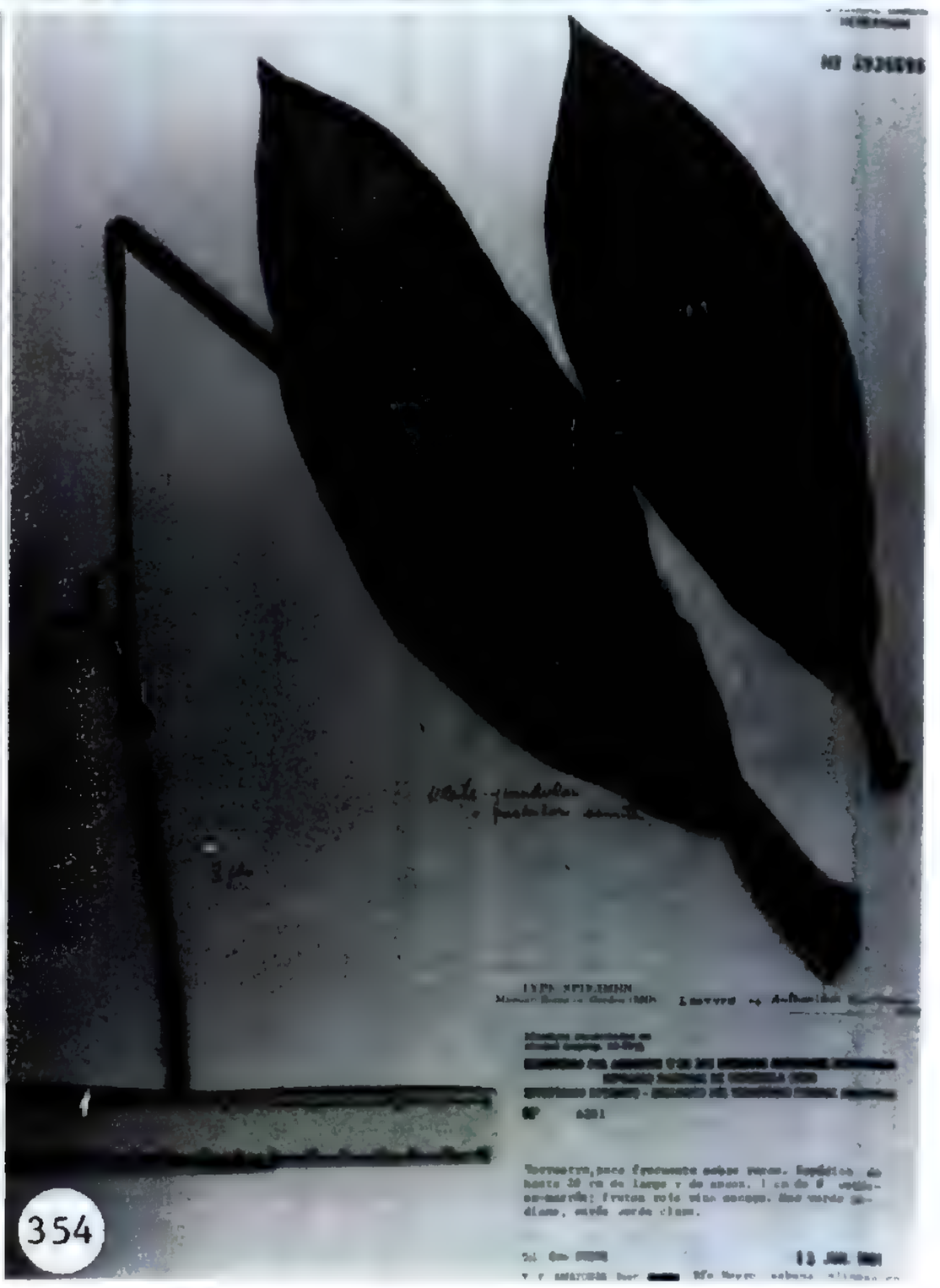

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MONOGRAPH OF THE NEOTROPICAL FERN GENUS *STIGMATOPTERIS* (DRYOPTERIDACEAE)[1]

Robbin C. Moran[2]

Abstract

Stigmatopteris contains 24 species with no varieties or subspecies. It is distinguished from all other genera of Dryopteridaceae (sensu stricto) by numerous punctate glands in the lamina, scales with uniseriate teeth or cilia, glandular cells terminating the apices of the teeth or cilia, and clavate vein apices that end behind the leaf margin. Other characteristics shared by all or nearly all species of the genus but also found in other dryopteroid ferns are nonindusiate sori, thin-textured leaves, glabrous laminar tissue, acuminate-serrate pinna, apices, thin, flaccid, tan or orangish scales, erect or short-creeping stems, and minutely pubescent adaxial grooves of the axes. Within the Dryopteridaceae, *Stigmatopteris* forms a clade with *Cyclodium*, *Olfersia*, and *Polybotrya*, held together by the synapomorphy of pubescent adaxial grooves of the axes. The genus is entirely neotropical and primarily montane, ranging from the Antilles and southern Mexico to southern Brazil but conspicuously absent from most of the Amazon basin. The Andes are the center of diversity for the genus, harboring eleven species, two of which are endemic. The coastal mountains of southeastern Brazil are another center, with six species, all of which are endemic. The Greater Antilles have also been important in the diversification of *Stigmatopteris* because they contain three species, all of which are endemic. All members of the genus grow in wet forests, generally from 200 to 2,000 m.

Resumen

Stigmatopteris contiene 24 especies sin subespecies ni variedades. Es distinguido de todos los otros géneros de las dryopteridáceas (sensu stricto) por las numerosas glándulas punctatas, escamas con dientes o cilias numerosas, células glandulares terminando los ápices de los dientes o cilias, y ápices clavatas de las venas que terminan atrás del margen de la lámina. Otras características compartidas por todas o casi todas las especies en el género, pero encontrado

[1] I thank Alan R. Smith (UC) for helpful discussions on all aspects of this work and Robert G. Stolze (F) for first pointing out to me that *Stigmatopteris* needed a modern monograph. Rolla M. Tryon (then at GH, now at USF) reviewed the nomenclatural parts of the species treatments and suggested improvements. Jorge V. Crisci (LP) provided assistance in running the HENNIG86 program used in the cladistic analysis of the species, and Enrique Forero (MO) and Warren D. Stevens (MO) facilitated funding for annotation labels and scanning electron microscopy. Gerrit Davidse (MO) and Henk van der Werff (MO) also provided support and encouragement for this project. I thank the curators of the following herbaria for making their specimens available for study: AAU, B, BM, CM, COL, CR, DUKE, F, G, GH, K, L, LIL, MICH, MU, NY, P, PH, PORT, QCNE, SI, UC, US, VEN, Z.

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también en otros helechos dryopteroides, son los soros no indusiados, hojas membranáceas, tejido de la lámina glabro, ápices de las pinnas acuminadas-seratas, escamas membranáceas, flacidas, pardas claras o naranjizas, rhizomas rectos o corte-reptantes, y los surcos adaxiales de la lámina cortamente pubescentes adentro. En las dryopteridaceas, *Stigmatopteris* hace un grupo monofilético con *Cyclodium*, *Olfersia*, y *Polybotrya*, basado en la sinapomorfía de surcos adaxiales pubescentes. El género es completamente neotropical y principalmente en regiones montañosas con bosques, extendiéndose desde las Antillas y sur de México hasta el sur de Brasil pero ausente de la mayoría de la cuenca Amazónica. Los Andes son el centro de diversidad para el género, con once especies, dos de las cuales son endémicas. Las montañas costales del sureste de Brasil son otro centro, con seis especies, todas las cuales son endémicas. Las Antillas han sido importante también en la diversificación de *Stigmatopteris*, con tres especies, todas de las cuales son endémicas. Todas las especies en el género existen en bosques húmedos, generalmente de 200 a 2,000 m.

Taxonomic History

Stigmatopteris was first proposed by Christensen in 1909. Until then, all of its species had been placed in *Dryopteris*, a genus that comprised a vast, unrelated assemblage of nearly 1,000 species. Four years later, in the first volume of his *Dryopteris* monograph, Christensen (1913) changed his mind about the rank of *Stigmatopteris*, placing it back in *Dryopteris* as a subgenus, but with the proviso that it could be treated, along with most of his other subgenera, as a distinct genus. Nowadays, pteridologists follow Christensen's original placement, giving *Stigmatopteris* full generic status.

Christensen's (1913) *Dryopteris* monograph also widened the definition of *Stigmatopteris* by including three species in what he informally called the "*Peltochlaena* group," which differed from true *Stigmatopteris* by having an indusium and a thick, nonglandular lamina. This group is now considered part of a separate genus, *Cyclodium*, which was recently monographed by Smith (1986). The species of *Cyclodium* previously placed in *Stigmatopteris* are listed in the excluded taxa section.

Geography

Stigmatopteris is entirely neotropical, extending from the Antilles and the state of Veracruz, Mexico, southward to southeastern Brazil (Fig. 1). The genus is absent from the Amazon basin except along the western portion adjacent to the Andes. It is primarily a montane genus, occurring in wet forests from 200 to 2,000 m, with the highest elevation being 2,500 m recorded for *S. rotundata* in Panama.

Species diversity and endemism in *Stigmatopteris* can be conveniently discussed using the regional centers of high endemism and species richness delimited by Tryon (1972) for tropical American ferns (Fig. 2). The region of highest diversity and endemism for the genus is the Andes, containing eleven species and two endemics (*S. ichthiosma*, and *S. pellucidopunctata*). Two species (*S. bulbifera* and *S. pterorachis*) are near-endemics, as they also occur outside the Andean Region in the Santa Marta Mountains of northern Colombia. Within the Andean Region, Colombia and Ecuador have more species (ten) than any other country (Tables 1, 2).

The coastal mountains of northern Venezuela have two species of *Stigmatopteris*, one of which is endemic (*S. nephrodioides*). Although these mountains do not harbor a large number of species, they could be considered a secondary regional center in Tryon's scheme because they have many endemic species.

The region with the next highest number of species is Central American, with seven species, one of which is endemic (*S. contracta*). With the exception of *S. contracta*, all of the other species extend southward into the Andean Region, giving the two regions a high floristic affinity.

Southeastern Brazil has played a major role in the diversification of *Stigmatopteris* because it has six species, all of which are endemic. The Greater Antilles have also been important, having three species, all of which are endemic.

The Guianan and Mexican centers contain few species and thus have not been important in the diversification of *Stigmatopteris*. The Mexican Region boasts one endemic (*S. chimalapensis*), but it is known only from one collection and may eventually be found outside of the region.

Morphology

Internal glands in the lamina. The glands can usually be seen with a dissecting microscope and, in oblique light, they appear as tiny raised bumps on the leaf surface (Fig. 3a, c). They often dry blackish. Perhaps the best way to see the glands

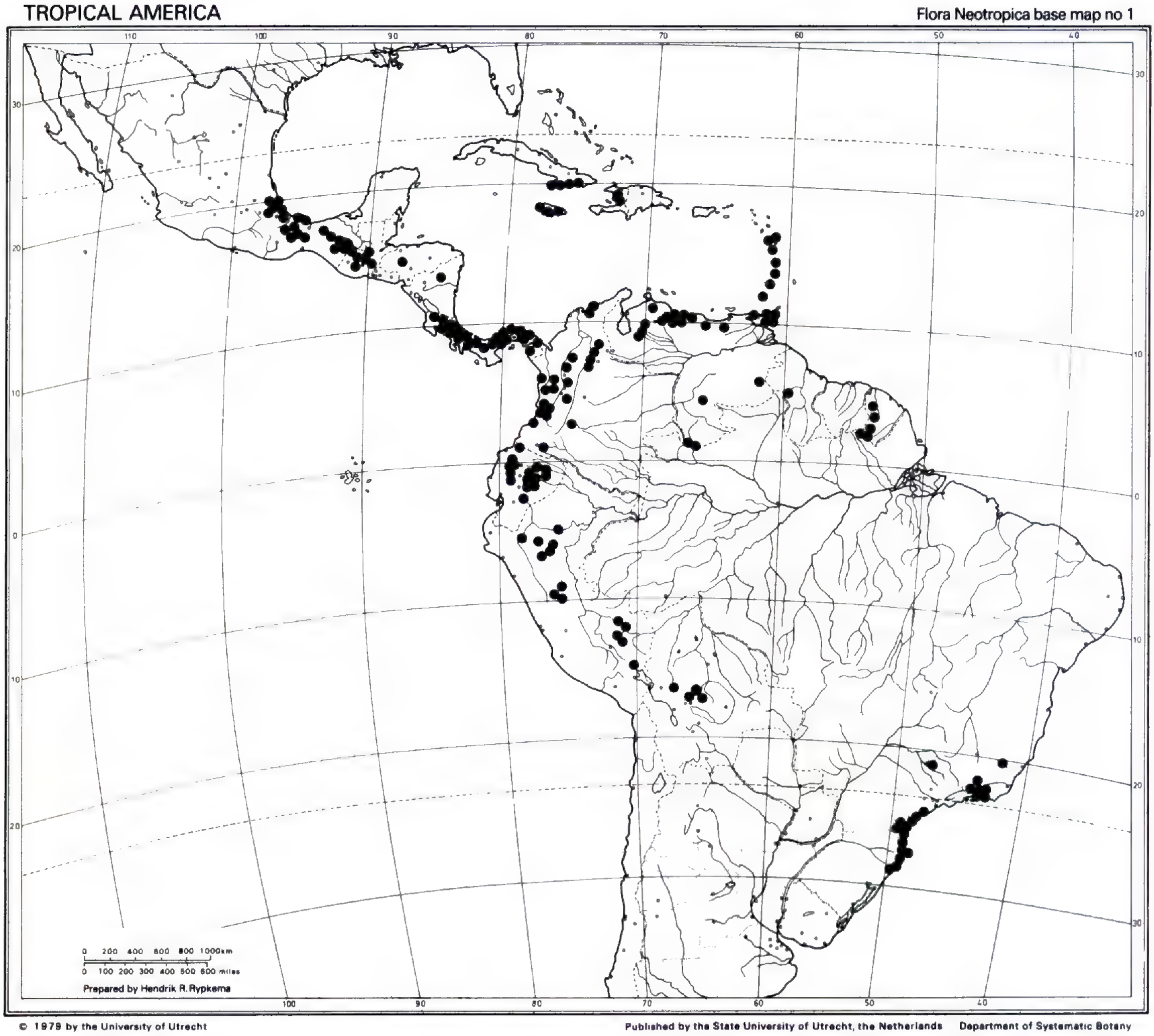


FIGURE 1. Distribution of *Stigmatopteris*.

is to look through a hand lens with the lamina illuminated from behind. Viewed this way, the glands appear as pellucid dots in the lamina (Fig. 3b). The glands are more conspicuous in some species than in others. Occasionally, they are so large and abundant that they are visible to the naked eye, but in *S. opaca*, a species with a thick lamina, the glands are not visible. The genus is named for these glands: from the Greek *stigmatos*, punctate, and *pteris*, fern.

Other genera of dryopteroid ferns also have internal glands, but these are extremely small and visible only by thin-sectioning and viewing under a compound microscope (Widén et al., 1983). The large glands in *Stigmatopteris* are probably homologous with these smaller ones, but nothing is known about the glands' structure, development, chemical contents, or role in metabolism.

Scales. The scale characteristic that distinguishes *Stigmatopteris* from all other genera of dryopteroid ferns is the presence of uniseriate cilia that end in a bulbous, often orange or brownish, glandular cell (Fig. 4). In other dryopteroid ferns, marginal teeth or processes are formed by the projecting end walls of two adjacent cells (Moran, 1987, fig. 7) and are never uniseriate or terminated by a glandular cell.

The scales of *Stigmatopteris* are more uniform than those in other genera of dryopteroid ferns. Although the shape differs, all species of *Stigmatopteris* have scales that are thin, flaccid, and tan or light orangish.

The scales decrease in size from the proximal to distal portions of the lamina until they become uniseriate or only 2–3 cells wide at the base (Figs. 4, 12b). These highly reduced scales, termed "proscales" or "microscales," are present on all species of the genus, and a dissecting microscope

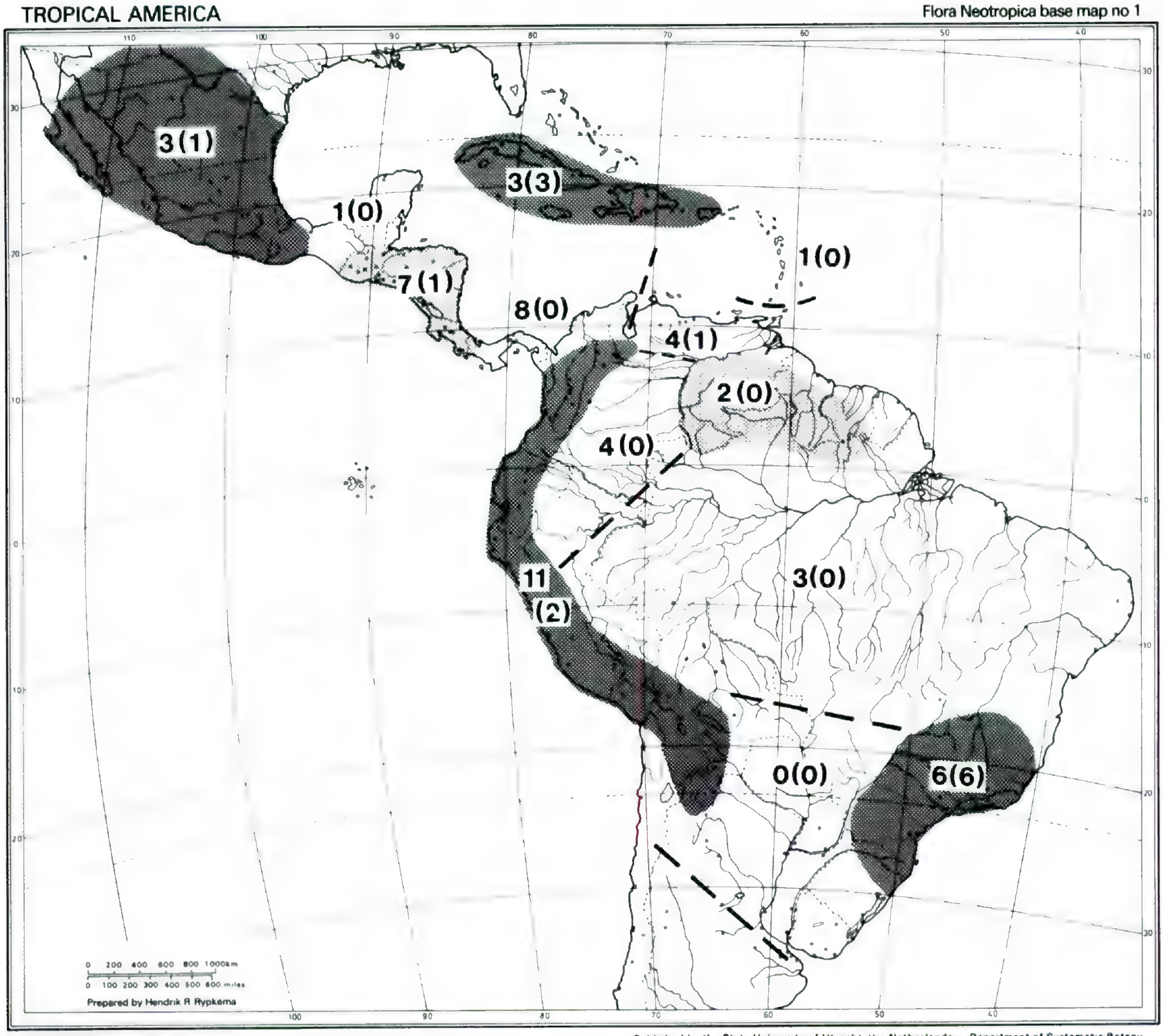


FIGURE 2. Distribution of *Stigmatopteris* species within regional centers of diversity and endemism for tropical American ferns defined by Tryon (1972). Primary centers are indicated with dark shading, secondary centers with light shading. The number on the left is the total number of species, and the number in parentheses indicates how many of those species are endemic.

is needed to see them. Their lateral processes are usually terminated by glandular cells.

Veins. Unlike most dryopteroid ferns, the veins of *Stigmatopteris* end behind the margin in clavate apices which are best seen adaxially (Fig. 23a). All other genera of dryopteroid ferns (sensu stricto) have the veins ending at or close to the margin, and the apices are slender, not thickened.

Indusia. *Stigmatopteris* is nonindusiate. Three species have an indusiumlike scale associated with the sorus (Figs. 17b, 18a), but these scales are certainly not homologous with the large, firm, thick-textured, circular indusia found in the outgroup genus *Cyclodium*. Although independently derived in *Stigmatopteris*, the lack of an indusium is not unique because many other dryopteroid ferns also lack an indusium.

Lamina shape and texture. All species have pinnae with long-acuminate apices that are serrate to the tip. The pinnae are equilaterally symmetrical, but some of the large species such as *S. contracta* and *S. lechleri* may have basal pinnae that are elongated basiscopically. The texture of the lamina is thin and papyraceous, except for that of *S. opaca*, which is thick and slightly chartaceous.

Hairs. All species of *Stigmatopteris* lack hairs except in the adaxial grooves of the rachis and costae. These hairs are 0.05–0.2 mm long, 1- or 2-celled, unbranched, and colorless to reddish. They are also found in the same position in *Cyclodium*, *Olfersia*, and *Polybotrya* and are a synapomorphy that holds these three genera and *Stigmatopteris* on the same clade within the Dryopteridaceae (see evolutionary relationships section). *Stigmatopteris heterophlebia* and *S. bulbifera*, however, are ex-

TABLE 1. Distribution of *Stigmatopteris* by country. Endemics are in boldface.

Mexico: 3 species, 1 endemic. **chimalapensis**, longicaudata, sordida.
Guatemala: 2 species, no endemics. longicaudata, sordida.
Honduras: 1 species, not endemic. longicaudata.
Nicaragua: 2 species, no endemics. heterophlebia, sordida.
Costa Rica: 5 species, no endemics. contracta, heterophlebia, killipiana, longicaudata, sordida.
Panama: 6 species, no endemics. contracta, heterophlebia, killipiana, longicaudata, michaelis, sordida.
Cuba: 1 species, 1 endemic. **hemiptera**.
Jamaica: 2 species, 1 endemic. gemmipara, **jamaicensis**.
Haiti: 1 species, not endemic. gemmipara.
Guadeloupe: 1 species, not endemic. rotundata.
Dominica: 1 species, not endemic. rotundata.
Martinique: 1 species, not endemic. rotundata.
St. Lucia: 1 species, not endemic. rotundata.
St. Vincent: 1 species, not endemic. rotundata.
Grenada: 1 species, not endemic. rotundata.
Trinidad: 1 species, not endemic. rotundata.
French Guiana: 1 species, not endemic. rotundata.
Guyana: 1 species, not endemic. longicaudata.
Venezuela: 5 species, 1 endemic. lechleri, longicaudata, **nephrodioides**, pterorhachis, rotundata.
Colombia: 10 species, no endemics. bulbifera, heterophlebia, ichthiosma, killipiana, lechleri, longicaudata, michaelis, pterorhachis, pellucidopunctata, sordida.
Ecuador: 10 species, no endemics. bulbifera, heterophlebia, ichthiosma, killipiana, lechleri, longicaudata, michaelis, opaca, pterorhachis, pellucidopunctata, sordida.
Peru: 5 species, no endemics. heterophlebia, lechleri, longicaudata, opaca, pellucidopunctata.
Bolivia: 2 species, no endemics. longicaudata, pellucidopunctata.
Brazil (southeastern): 6 species, 6 endemics. **brevinervis**, **caudata**, **heterocarpa**, **prionites**, **tyucana**, **ulei.**

TABLE 2. The species of *Stigmatopteris* and their distribution by country.

1. *S. brevinervis* (Fée) R. C. Moran: southeastern Brazil.
2. *S. bulbifera* R. C. Moran: Colombia, Ecuador.
3. *S. caudata* (Raddi) C. Chr.: southeastern Brazil.
4. *S. chimalapensis* Mickel & Beitel: southern Mexico.
5. *S. contracta* (Christ) C. Chr.: Costa Rica, Panama.
6. *S. gemmipara* C. Chr.: Jamaica, Haiti.
7. *S. hemiptera* (Maxon) C. Chr.: Cuba.
8. *S. heterocarpa* (Fée) Rosenstock: southeastern Brazil.
9. *S. heterophlebia* (Baker) R. C. Moran: Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru.
10. *S. ichthiosma* (Sodiro) C. Chr.: western Ecuador.
11. *S. jamaicensis* (Desv.) Proctor: Jamaica.
12. *S. killipiana* Lellinger: Costa Rica, Panama, Colombia, Ecuador.
13. *S. lechleri* (Mett.) C. Chr.: Costa Rica, Venezuela, Colombia, Ecuador, Peru.
14. *S. longicaudata* (Liebm.) C. Chr.: Mexico, Guatemala, Honduras, Costa Rica, Panama, French Guiana, Venezuela, Colombia, Ecuador, Peru, Bolivia.
15. *S. michaelis* (Baker) C. Chr.: Panama, Colombia, Ecuador.
16. *S. nephrodioides* (Klotzsch) C. Chr.: Venezuela.
17. *S. opaca* (Baker) C. Chr.: Ecuador, Peru.
18. *S. pellucidopunctata* (C. Chr.) C. Chr.: Colombia, Ecuador, Peru, Bolivia.
19. *S. prionites* (Kunze) C. Chr.: southeastern Brazil.
20. *S. pterorhachis* R. C. Moran: Venezuela, Colombia.
21. *S. rotundata* (Willd.) C. Chr.: Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, Grenada, Trinidad, French Guiana, Guyana, Venezuela.
22. *S. sordida* (Maxon) C. Chr.: Mexico, Guatemala, Nicaragua, Costa Rica, Panama, Colombia, Ecuador.
23. *S. tyucana* (Raddi) C. Chr.: southeastern Brazil.
24. *S. ulei* (Christ) Sehnem: southeastern Brazil.

ceptions to the general condition of hairlessness in the genus because their axes are covered abaxially with capitate-glandular hairs.

Sporangia. The sporangia are like those described by Moran (1987) for *Polybotrya*, except that the stalks lack a hairlike paraphysis.

Petiole anatomy. A cross section of the petiole shows that the vascular bundles are arranged in a mushroomlike outline, with the base of the mushroom oriented adaxially (Fig. 12a). This is typical of dryopteroid ferns (Moran, 1986, 1987; pers. obs.). Aerophores run down the sides of the petiole and are evident in cross section by a gap in the thickened peripheral collenchyma of the petiole. The petiole bases do not persist or accumulate starch after the rest of the leaf has withered. In other words, *Stigmatopteris* lacks trophopods.

Spores. I examined the spores from 11 species of *Stigmatopteris* with the scanning electron microscope (SEM). All of the spores were typical of those found elsewhere in the Dryopteridaceae, being monolete, having a smooth exospore, and showing a broadly inflated or narrowly folded perispore (Fig. 5). The inner layer of the perispore is thin and usually adheres to the smooth exospore; the outer layer is thicker and compact.

The perisporal surface on and between the folds was nearly uniform in all 11 species examined (Fig. 5). The surface is relatively unornamented, being either smooth (Fig. 5f) or beset with low, diffuse ridges (Fig. 5c, d). Because of the uniformity, the spores do not provide helpful characters in the subgeneric taxonomy of the genus.

Ornamentation of the perispore differs in *Stigmatopteris* from that of the most closely related

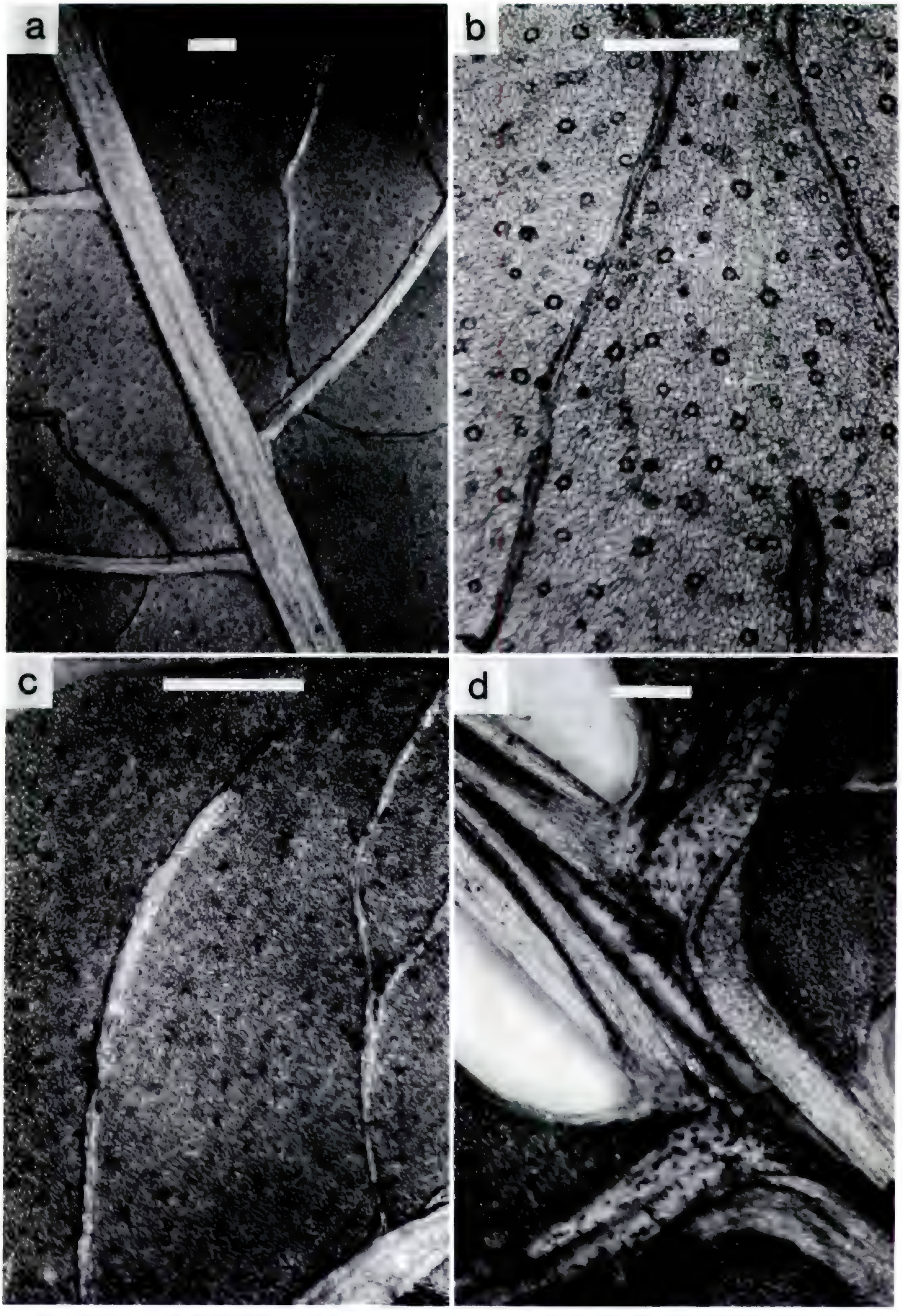


FIGURE 3. Internal punctate glands in the lamina of *Stigmatopteris* (a–c) and rachis-costa juncture showing adaxial grooves pubescent with short hairs (d). White bars indicate 1 mm.—a, b. *S. bulbifera* (*Øllgaard et al. 35866*, AAU).—c. *S. contracta* (*Moran 3330*, MO).—d. *S. heterocarpa* (*Haerchen 106*, B).

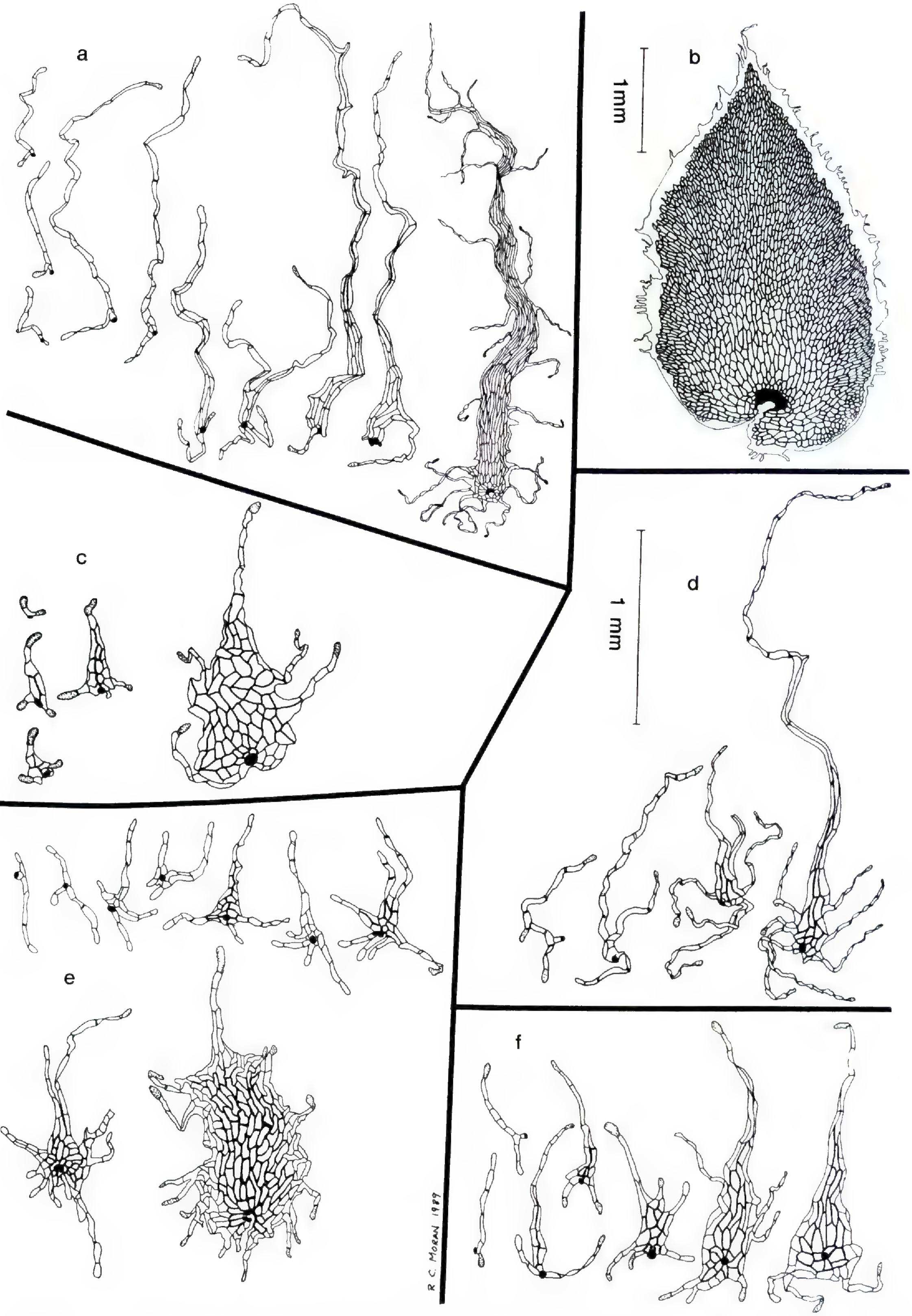
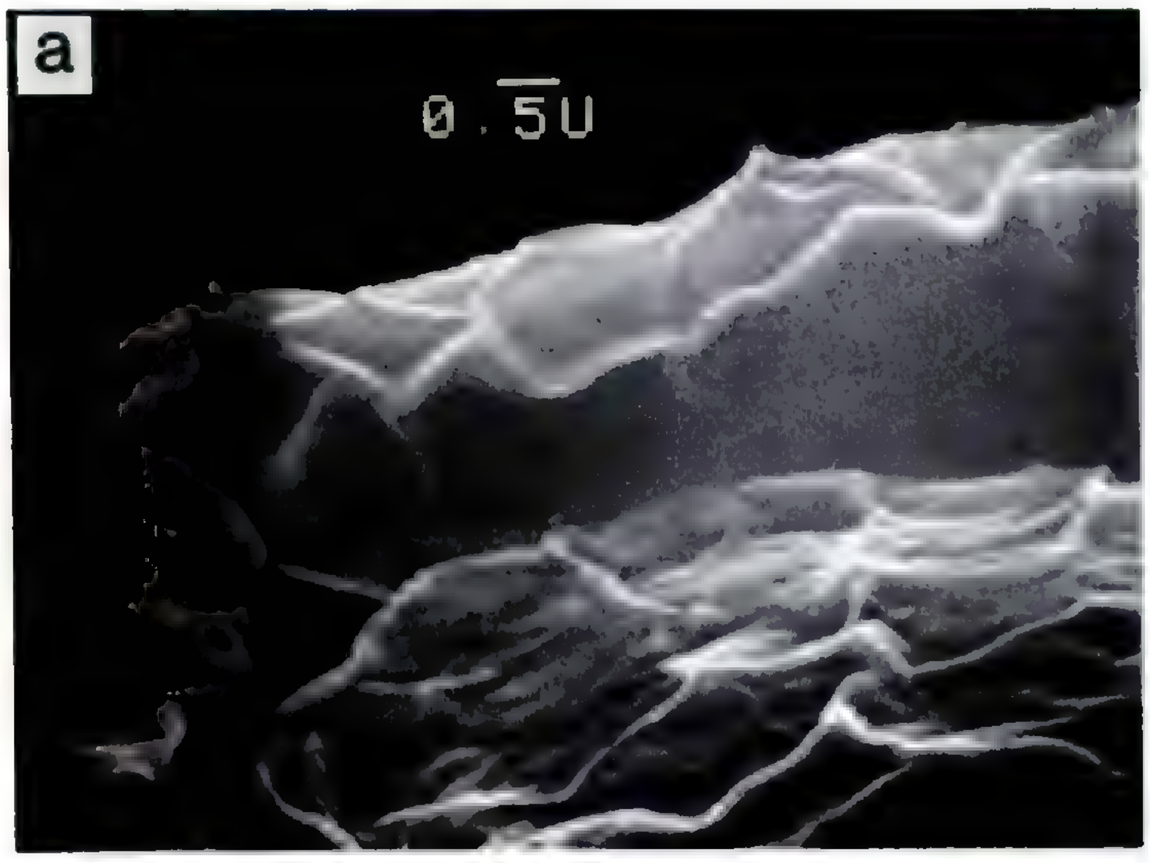


FIGURE 4. Scales of *Stigmatopteris*. The scale shown in b is from a petiole base; all others are from the abaxial surface of the lamina and show the transition from uniseriate scales (proscales or microscales) to multiseriate ones. All are the same magnification as shown in d, except b and the far right scale in a.—a. *S. pellucidopunctata* (*Moran 3624*, MO).—b. *S. ichthiosma* (*Moran 3545*, MO).—c. *S. sordida* (*Gómez 18641*, CR).—d. *S. lechleri* (*Moran 3582*, MO).—e. *S. opaca* (*Moran 3576*, MO).—f. *S. sordida* (*Moran 3315*, MO).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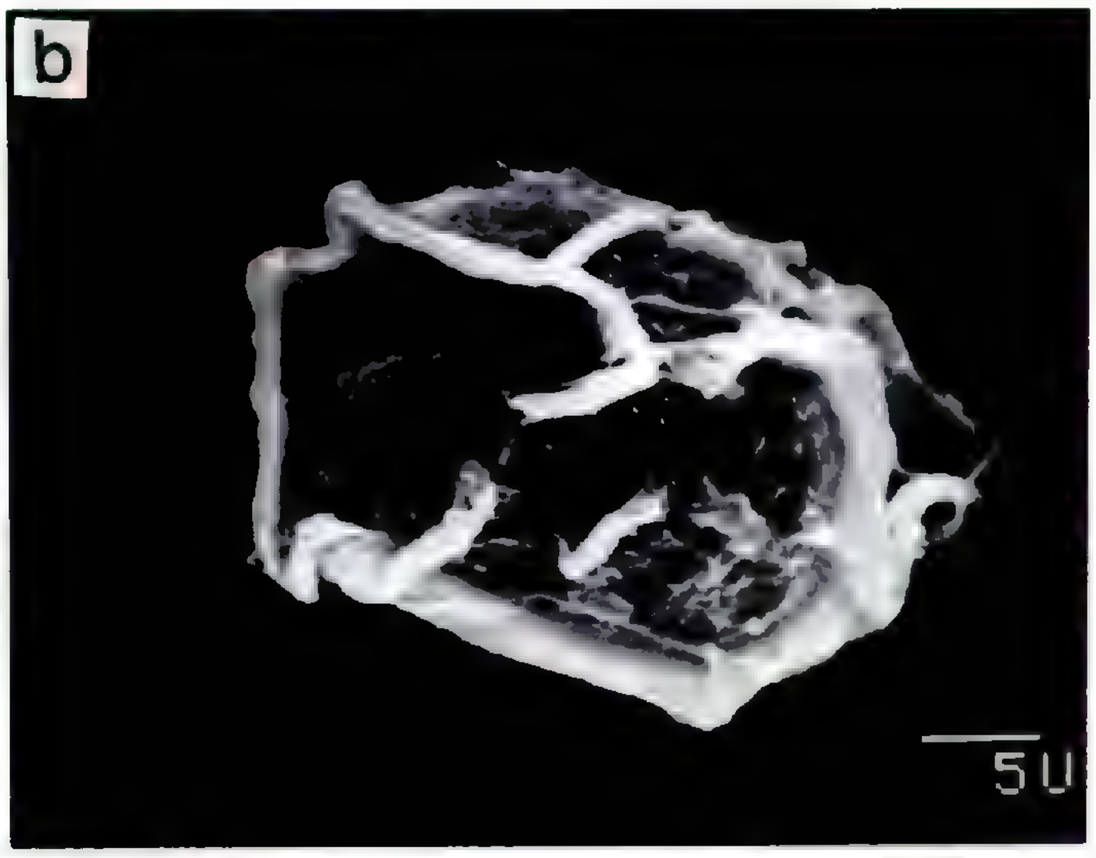
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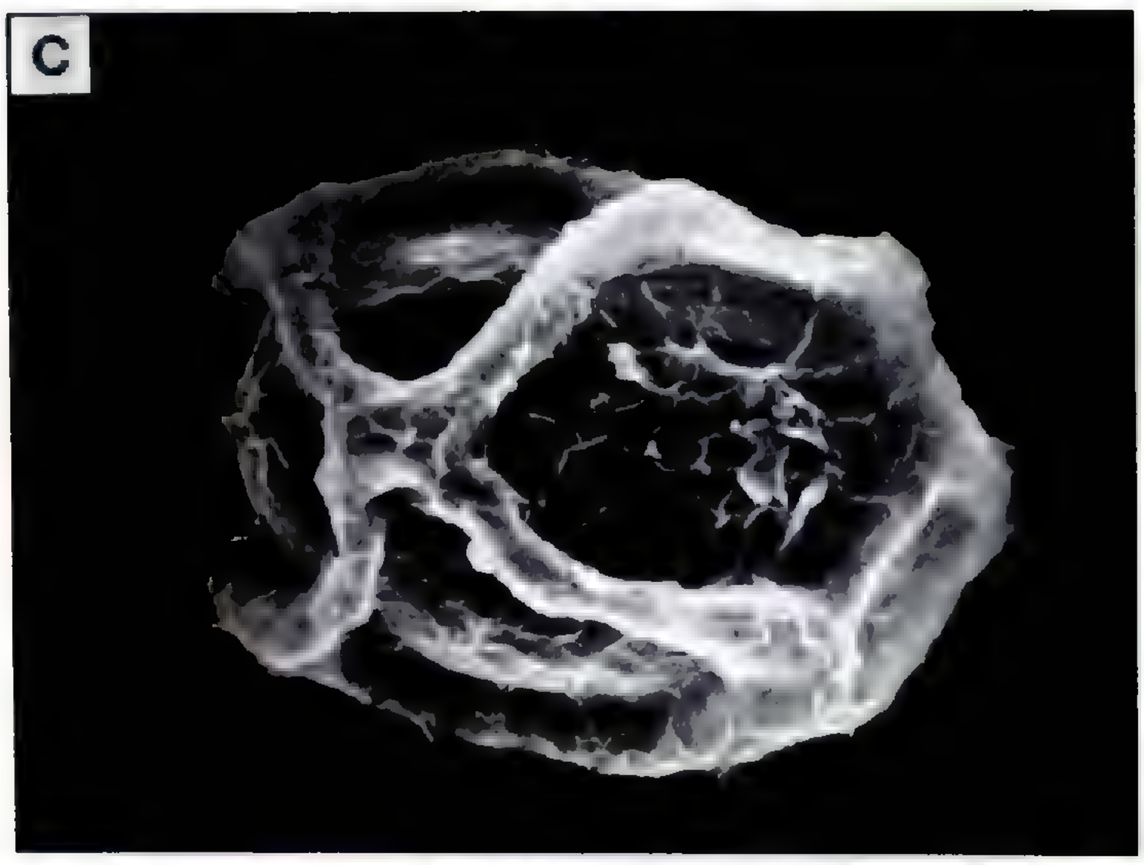
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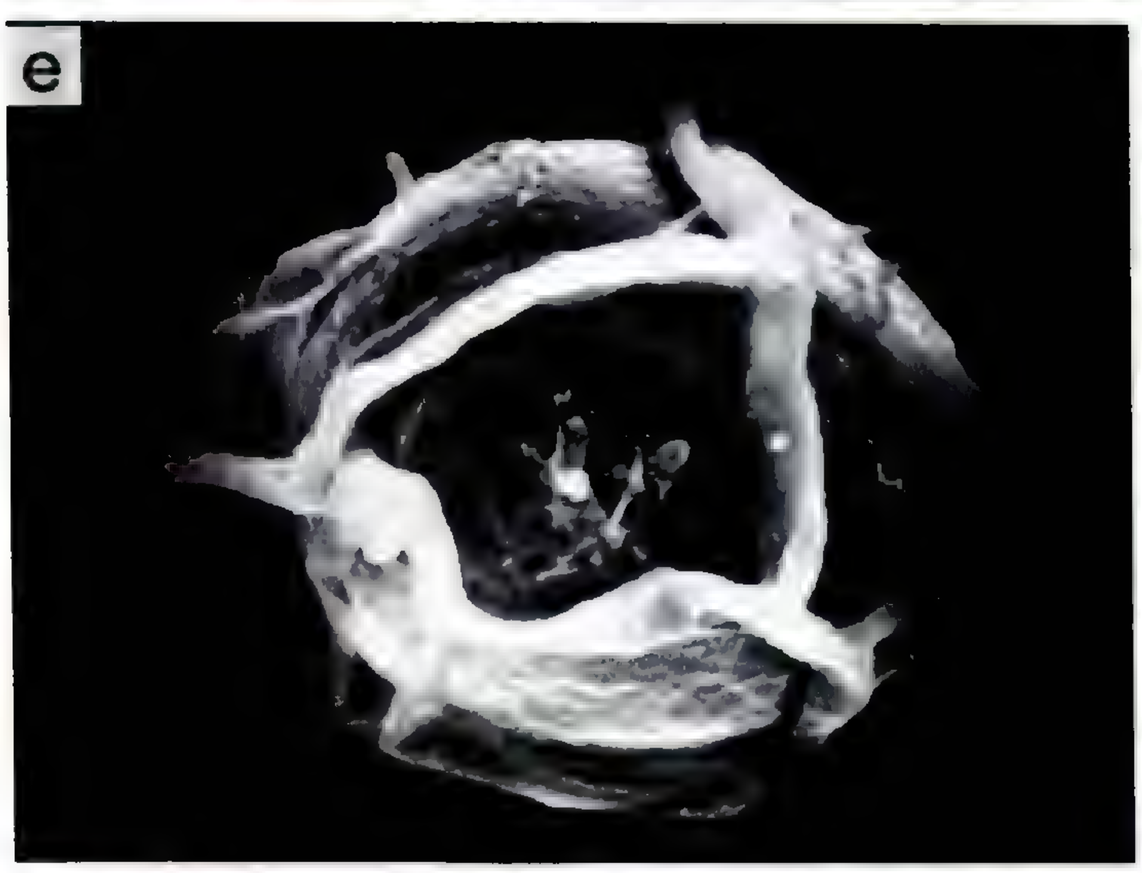
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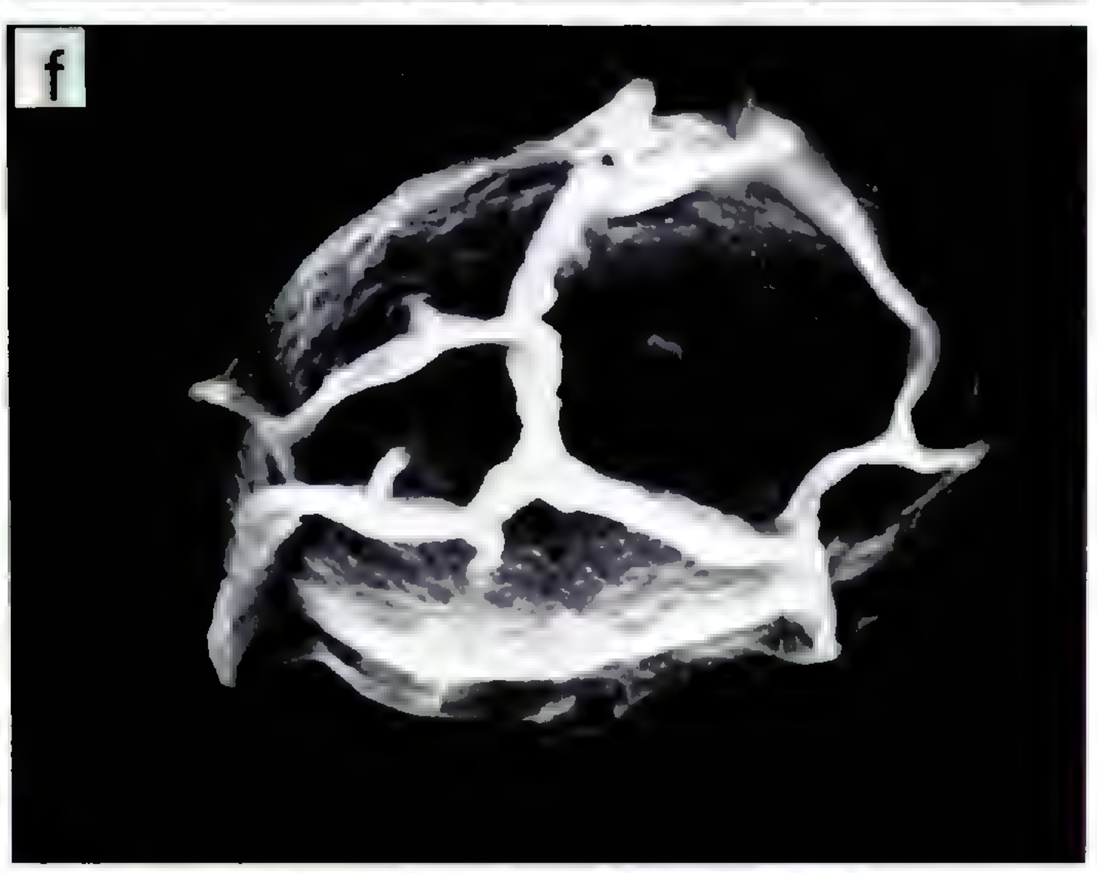
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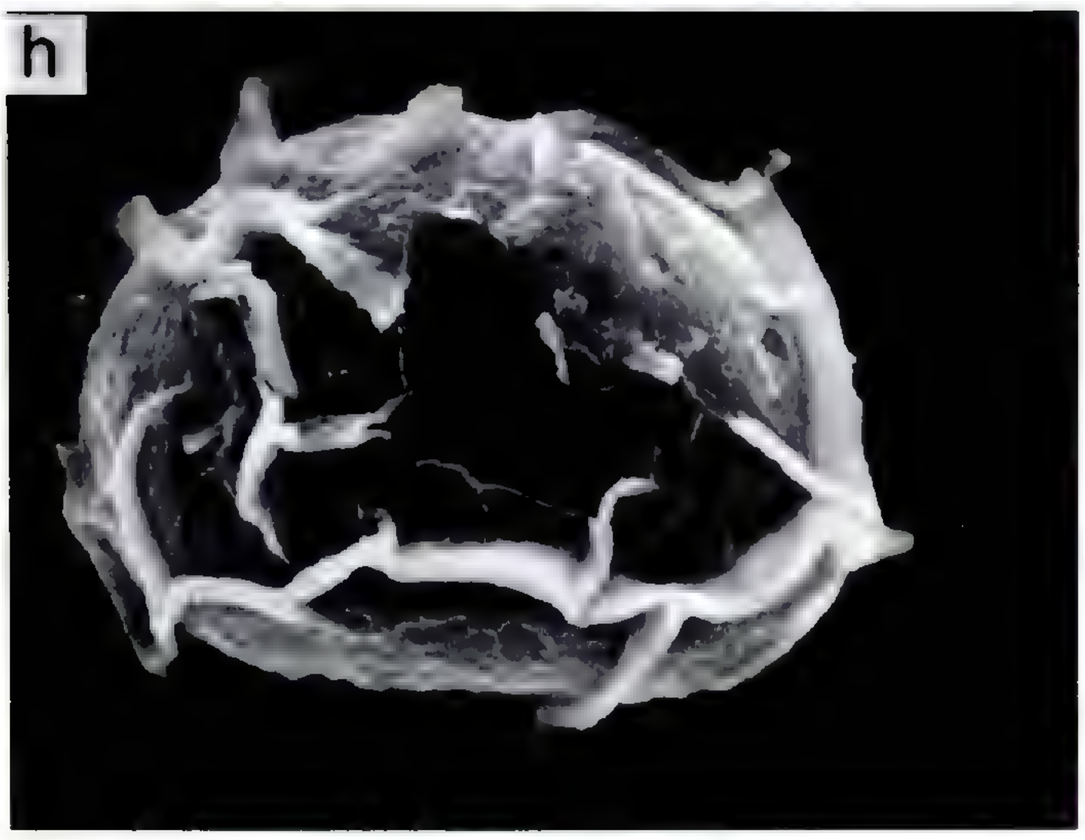
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dryopteroid genera, i.e., *Polybotrya*, *Cyclodium*, and *Olfersia*. These genera have more ornamentation on the perispore. For example, the spores of *Polybotrya* are typically densely echinate (Moran, 1987; Tryon & Tryon, 1982); those of *Cyclodium* are usually finely papillate but can be variously ornamented (Smith, 1986; Tryon & Tryon, 1982); and those of *Olfersia* are sparsely echinate (Moran, 1986; Tryon & Tryon, 1982).

Although these types of spore ornamentation are distinct, it is premature to determine which type is ancestral and which is derived. Such a determination must await a comprehensive comparative study of perisporal ornamentation in the Dryopteridaceae. Therefore, I have not used spore ornamentation in the cladogram for *Stigmatopteris* and related genera (Fig. 6).

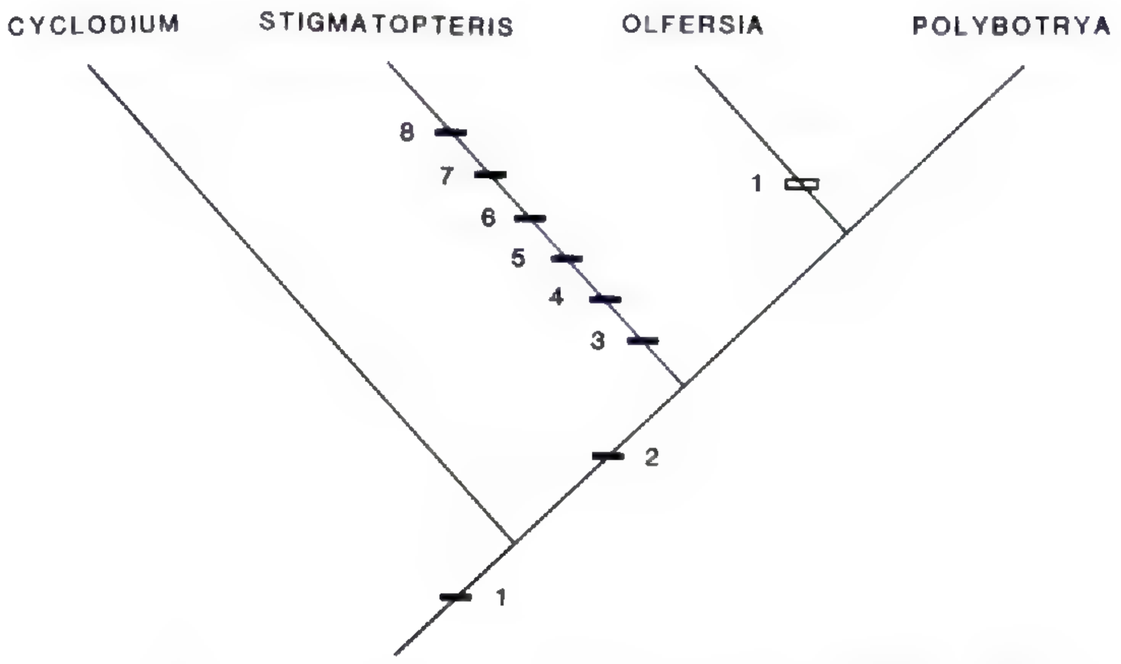


FIGURE 6. Cladogram of *Cyclodium*, *Stigmatopteris*, *Olfersia*, and *Polybotrya*. The numbered black bars represent the derived character states given in Table 4. The open bar below *Olfersia* represents a character state reversal. See Moran (1986) for the additional apomorphies and synapomorphies pertaining to *Olfersia* and *Polybotrya*.

CHROMOSOME NUMBER

Walker (1966), who has made the only chromosome count for *Stigmatopteris*, found that $n = 41$ in *S. jamaicensis* (reported as *S. nothochlaena*, a synonym). This number relates the genus to the dryopteroid ferns.

Walker also noted that meiosis occurs very early in *Stigmatopteris* during the crozier stage of leaf development. Unfortunately, most workers (including myself) have collected samples for chromosome counts past the crozier stage, at a stage more typical for ferns in general, i.e., when the sori are small and white, but on expanded leaves beyond the crozier stage. This probably explains why only one count exists for the genus.

EVOLUTIONARY RELATIONSHIPS

Family relationships. That *Stigmatopteris* is a member of the Dryopteridaceae (sensu stricto of Holttum, 1984) is clearly shown by several characteristics which it shares with all genera of that family: $x = 41$, more than three vascular bundles in the petiole and these arranged in an omega shape when viewed in cross section (Fig. 12a), and grooves on the adaxial surface of the axes that are decurrent into those of the next lower order. The Dryopteridaceae are closely related to the Tectariaceae (sensu stricto of Holttum, 1984), but *Stigmatopteris* differs from the latter family by lacking *Cteni-tis* hairs (i.e., small catenate, several-celled hairs with the color aggregated in the cross walls), and having sulcate, decurrent axial grooves.

Generic relationships. *Stigmatopteris* most closely resembles *Cyclodium* (sensu Smith, 1986), another dryopteroid genus, as shown by similarities in leaf cutting and venation and by the laminae, which are hairless except for the grooves of the rachis and costae. In fact, the two genera are so similar in these respects that some pteridologists (e.g., Christensen, 1913, 1920; Tryon & Tryon, 1982) have regarded them as one. They are, however, best kept as distinct. The two genera exhibit 11 morphological differences (Table 3), and this is more than that which occurs between other pairs of dryopteroid genera, such as *Arachniodes* and *Dryopteris*, *Arachniodes* and *Maxonia*, or *Cyrtomium* and *Polystichum*. If there is to be consistency in recognizing dryopteroid genera, at least as regards the number of characters that separate them, then *Cyclodium* and *Stigmatopteris* should be maintained as distinct.

In the Dryopteridaceae, *Stigmatopteris* and *Cyclodium* form a clade with *Polybotrya* and *Olfersia* (Fig. 6, Table 4). This clade is defined by the presence of hairs in the adaxial grooves of the axes (Fig. 3d). This character state is considered synapomorphic because all other dryopteroid ferns (sensu stricto) are hairless in the adaxial grooves of the axes. This character state would be weak if

←

FIGURE 5. Spores of *Stigmatopteris*.—a, c. *S. longicaudata* (*Mickel 6392*, NY).—b. *S. lechleri* (*von Sneidern 5046*, US).—d. *S. tyucana* (*Brade 5892*, NY).—e. *S. opaca* (*Øllgaard et al. 35859*, AAU).—f. *S. sordida* (*Moran 3315*, MO).—g. *S. rotundata* (*Cremers 9140*, UC).—h. *S. caudata* (*Webb s.n.*, NY). Spores c–h the same scale as in b.

TABLE 3. Comparison of *Stigmatopteris* and *Cyclodium*.

SIMILARITIES
Hairs of the lamina: lacking (except in grooves of the rachis and costae).
Hairs in grooves of the rachis and costae: 0.05–0.2 mm long, usually blunt-tipped, colorless, one- to few-celled.
Lamina cutting: similar in many species, cf. *S. rotundata* and *C. guianense*, or *S. opaca* and *C. meniscioides*.
Venation: similar in free-veined species such as *S. nephrodioides* and *C. guianense*, and in anastomosing-veined species such as *S. heterophlebia* and *C. meniscioides*.

DIFFERENCES		
Character	*Stigmatopteris*	*Cyclodium*
Indusium:	absent	present
Lamina texture:	papyraceous	chartaceous or coriaceous
Pinnule arrangement:	anadromous basally, catadromous distally	anadromous throughout
Position of vein ending:	behind margin	at margin
Shape of vein tips:	clavate	slender
Internal laminar glands:	present	absent
Scale frequency on axes:	common	rare or lacking
Scale color:	light brown or orangish	dark brown
Scale texture:	thin	thick
Marginal teeth of scales:	uniseriate	composed of upturned margins from two adjacent cell walls
Gland at the apex of scale teeth:	present	absent
Geography:	primarily Andean	primarily Guianan

nothing else correlated with it; it could have evolved more than once, and if so the clade would be polyphyletic. The hypothesis that this character evolved only once is supported by the fact that the type of pubescence is the same in all the genera: the hairs are 0.05–0.2 mm long, usually blunt-tipped, colorless, and one- to few-celled (Smith, 1986; Moran, 1987, fig. 10b–e, g, h). *Olfersia cervina*, the only species of *Olfersia*, is an exception, having glabrous grooves. Because *Olfersia* is the sister genus to *Polybotrya* (Moran, 1986), its lack of hairs in the grooves is best interpreted as a character state reversal (Fig. 6). Some species of *Polybotrya* subg. *Polybotrya*, such as *P. osmundacea* and *P. cyatheoides*, have much longer hairs in the grooves (Moran, 1987, fig. 49c) than those found in the grooves of *Cyclodium* and *Stigmatopteris*. These longer hairs, however, are otherwise similar to the smaller ones and are probably derived from them.

The clade with *Stigmatopteris*, *Olfersia*, and *Polybotrya* is defined only by one synapomorphy: loss of the indusium (Fig. 6, Table 4). This synapomorphy is weak and therefore considered tentative because no others correlate with it. Furthermore, the number of times the indusium has been lost in

TABLE 4. Characters and character states used in the cladistic analysis of *Stigmatopteris*, *Cyclodium*, *Olfersia*, and *Polybotyra* (Fig. 6). Character state polarities were determined by comparison to other genera in the Dryopteridaceae, such as *Arachniodes*, *Dryopteris*, and *Polystichum*.

Character	Ancestral condition	Derived condition
1. Pubescence in adaxial grooves of the axes	absent	present
2. Indusium	present	absent
3. Large glands in the lamina	absent	present
4. Marginal teeth or processes of the scales	composed of the upturned margins from two adjacent cells	uniseriate
5. Glandular cell at apex of scale teeth or processes	absent	present
6. Vein termination	at margin	behind margin
7. Shape of vein tip	slender	clavate
8. Texture of lamina	papyraceous or chartaceous	membranaceous

TABLE 5. Data matrix used in the cladistic analysis of 23 species of *Stigmatopteris*, with *Cyclodium* used as the outgroup. See Table 6 for the meaning of characters and character states.

Taxon	Characters								
	1	2	3	4	5	6	7	8	9
Cyclodium	0	0	0	0	0	0	0	0	0
S. pterorhachis	0	0	1	1	4	0	0	0	1
S. bulbifera	0	1	1	1	4	0	1	0	1
S. heterophlebia	0	0	1	1	4	0	1	0	1
S. killipiana	0	0	1	0	4	0	0	0	1
S. opaca	0	0	1	0	4	0	0	0	1
S. longicaudata	0	0	0	1	4	0	0	0	0
S. heterocarpa	0	0	0	0	4	0	0	0	0
S. rotundata	0	0	0	0	3	0	0	0	0
S. prionites	0	0	0	0	3	0	0	0	0
S. nephrodioides	0	0	0	0	3	0	0	0	0
S. michaelis	0	0	0	1	2	0	0	0	0
S. tyucana	0	0	0	0	3	0	0	0	0
S. chimalapensis	0	0	0	0	3	0	0	0	0
S. jamaicensis	1	0	0	0	1	0	0	0	0
S. hemiptera	0	1	0	0	2	1	0	0	0
S. gemipara	0	1	0	0	2	0	0	0	0
S. brevinervis	0	0	0	0	2	0	0	0	0
S. contracta	1	0	0	0	1	0	0	1	0
S. caudata	0	0	0	0	1	1	0	0	0
S. ichthiosma	1	0	0	0	1	0	0	1	0
S. sordida	0	0	0	0	2	0	0	1	0
S. pellucidopunctata	0	0	0	0	2	0	0	1	0
S. lechleri	0	0	0	0	0	0	0	0	0

fern evolution suggests that it could have easily been lost independently in *Stigmatopteris* and in the *Olfersia–Polybotrya* clade.

Species relationships. A cladogram of species relationships was constructed using the HENNIG86 program, version 1.5 (Farris, 1988; Platnick, 1989), run on a Dell System 200 computer applying the implicit enumeration option for calculating trees. Table 5 shows the data matrix used in the analysis, and Table 6 lists the characters and character states used in the data matrix. *Stigmatopteris ulei* was not included in the data matrix because it appears to be of hybrid origin. Another feature of HENNIG86 was also used: the successive weighting procedure, which calculates weights from the best fits to the most parsimonious trees using rescaled consistencies (rc), which are the products of the character consistency (c) and the character retention index (r). The product is scaled to lie in the range 0–10 (Table 7). The weighting procedure is repeated on successively produced trees until the trees no longer change (Farris, 1988).

Cyclodium was used as the outgroup to determine character state polarities in Table 6 (see section on generic relationships for justification of using *Cyclodium* as the outgroup). All species of *Cyclodium* have the ancestral character states given in Table 4 for characters 1, 2, 4, 6, 7, and 8; therefore, it was simple to determine polarity. However, because *Cyclodium* has both character states for characters 3, 5, and 9 (Table 6), it could not be used to determine character state polarity. For

TABLE 6. Characters and character states used in the cladistic analysis of 23 species of *Stigmatopteris* (the probable hybrid *S. ulei* not included). The ancestral state equals 0; the derived state (s) equals 1 (or more). The hypothesized evolutionary pathways for all the character states are unilinear.

1. Indusial scale: absent (0); present (1).
2. Buds: absent (0); 1 = present (1).
3. Veins: free (0); anastomosing (1).
4. Distal pinnae bases: short-decurrent (0); long-decurrent (1).
5. Lamina dissection: 2-pinnate-pinnatifid (0); nearly 2-pinnate (1); pinnae cut ½–¾ to the costa (2); pinnae cut ½–¾ to the costa (3); entire or nearly so (4).
6. Basal basiscopic lobe of the distal pinnae: adnate to costa (0); adnate to the rachis (1).
7. Hairs on rachis and costa: absent (0); present (1).
8. Petiole scale texture: thin, flaccid (0); thick, rigid (1).
9. Number of pinna pairs: 12–18 (0); 1–12 (1).

TABLE 7. Character consistencies (c) and retention indices (r) as the best fits on the three equally parsimonious trees from HENNIG86, which was used to calculate weights. Final weights were often the third round of successive weighting procedures in HENNIG86. Weights were truncated to integers.

Character	Range of steps	Number of steps	Consistency index (c)	Retention index (r)	Weight (rc × 10)	Final weight
1	1	1	1	1	10	10
2	1	2	0.5	0.5	2	2
3	1	1	1	1	10	10
4	1	3	0.3	0.5	1	1
5	4	4	1	1	10	10
6	1	2	0.5	0	0	0
7	1	1	1	1	10	10
8	1	2	0.5	0.7	3	3
9	1	1	1	1	10	10

these three characters, polarity was determined by deferring to Holttum's (1968) hypotheses about the general trends in fern evolution. This method is not entirely satisfactory, but in this case it is the best that could be done with present knowledge.

Regarding character 3 (free vs. anastomosing veins), Holttum (1968) believed that the evolutionary trend has been from free to anastomosing. Therefore, free veins were assigned as the ancestral character state (Table 6). He also believed that the earliest ferns had highly divided leaves and that the evolutionary trend has been toward less divided leaves. Accordingly, character 5 (leaf division) has the most divided leaf as the ancestral state and the least divided leaf (1-pinnate with entire pinnae) the derived state. Finally, for character 9, Holttum believed that the evolutionary trend has been to develop fewer pinnae; therefore, the smaller number of pinnae was considered as the derived state.

HENNIG86 found three equally most-parsimonious cladograms (Fig. 7), which differed only in the branching patterns for seven of the most derived species—a group that consists primarily of species with anastomosing veins and entire to shallowly lobed pinnae. All of the trees had 17 steps and a consistency index of 0.7. Cladogram 2 (Fig. 7) has two character state sequences. The one shown involves a reversal of character 4 at the node that defines *S. opaca* and *S. killipiana*. The other sequence assumes a parallelism of character state 4.1 at the line leading to *S. longicaudata* and at the node which defines *S. pterorhachis*, *S. bulbifera*, and *S. heterophlebia*. I do not believe that one of these sequences is more likely than the other; both seem equally probable.

At the beginning of this study, I thought that species from different regions might form monophyletic groups, such as the six species from southeastern Brazil, or the three species from the Greater Antilles, or the eleven species from the Andes. Although two of the species endemic to the Greater Antilles proved to be sister species, no general correlation exists between the cladogram and the geography of the other species. In other words, no synapomorphy exists that holds together the species from these regions.

The species with anastomosing veins and entire to shallowly lobed pinnae are distinctive and form a monophyletic group (Fig. 7, trees 1, 2, 3). They could be considered a subgenus, much the same way that *Soromanes* is considered a subgenus of *Polybotrya* (Moran, 1987). However, *S. longicaudata* is intermediate between the group and the rest of the genus, and so I have not formally named the group.

Key and Descriptions

Stigmatopteris C. Chr., Bot. Tidsskr. 29: 292. 1909. TYPE: *Stigmatopteris rotundata* (Willd.) C. Chr.

Dryopteris subg. *Stigmatopteris* (C. Chr.) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 7, 10: 73. 1913.

Plants terrestrial; rhizome short-creeping, scaly at the apex, the meristeles surrounded by whitish parenchyma (not darkened sclerenchymatous sheaths); petioles with 4 to many vascular bundles in cross section (Fig. 12a), continuous (not articulate) with the rhizome; lamina 1-pinnate to 2-pinnate-pinnatifid, the apex pinnatifid, the tissue glabrous on both surfaces, with punctate glands in the mesophyll (Fig. 3a–c); pinnae linear to narrowly oblong, often with a decurrent basal wing, the apices attenuate and serrate; pinnae or segments arranged anadromically in the proximal pinna pairs, becoming catadromically arranged in the distal pinna pairs; adaxial surface of the rachis and costae sulcate, the sulci decurrent into those of the next lower order, pubescent adaxially within the grooves (Fig. 3d), the hairs 0.05–0.2 mm, 1- or 2-celled, colorless, usually blunt-tipped; abaxial surface of the rachis and costae stramineous or occasionally brown, lacking hairs abaxially or (in two species) glandular-pubescent, scaly, the scales thin, translucent, light brown to orangish, ciliate or denticulate, the cilia or teeth terminating in a

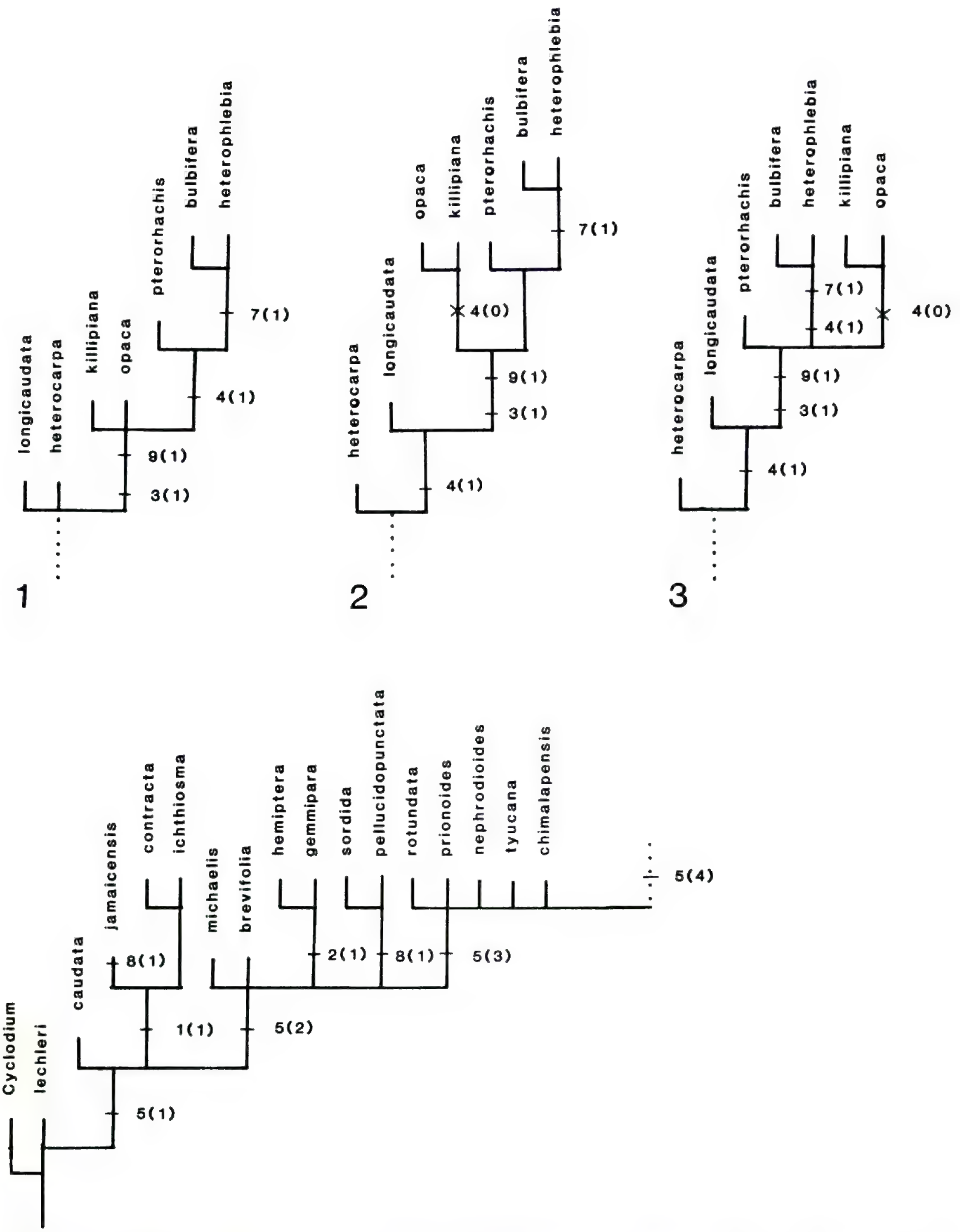


FIGURE 7. Cladogram of species relationships in *Stigmatopteris*. Cladograms 1, 2, and 3 attach to dotted far right of the bottom tree. Cross bars indicate apomorphies; the × in cladograms 2 and 3 indicate reversals.

darkened, slightly enlarged, glandular cell (Fig. 4); veins either free or inconsistently anastomosing (i.e., mostly anastomosing but with a readily noticeable number of free veins), the tips clavate adaxially (hydathodous?), terminating before the margin; sori round or slightly oblong near the costae; indusia absent; sporangial stalks not paraphysate; spores monolete, with broadly folded perispore and low, broken ridges (Fig. 5). Chromosome number, $x = 41$.

KEY TO THE SPECIES OF *STIGMATOPTERIS*

1a. Key to the species of the Antilles and southeastern Brazil.
2a. Species of the Antilles.
3a. Pinnae crenate or cut less than ⅓ to the costa; Lesser Antilles ..... 21. *S. rotundata* (Willd.) C. Chr.
3b. Pinnae cut ½–⅞ to the costa; Greater Antilles.
4a. Pinnae with the basal basiscopic lobe arising from the rachis (Fig. 14a); Cuba ..... 7. *S. hemiptera* (Maxon) C. Chr.
4b. Pinnae with the basal basiscopic lobe arising from the costa; Jamaica, Haiti.
5a. Lamina lacking buds; pinnae 15–23 cm, pairs 22–26; veins 8–11 per segment; sori covered by an indusiumlike scale; petiole ca. half the length of the lamina; Jamaica ..... 11. *S. jamaicensis* (Desv.) Proctor
5b. Lamina bearing buds; pinnae (4–)9–14 cm, pairs 9–20; veins 5–7(–8) per segment; sori lacking an indusiumlike scale; petiole equaling the length of the lamina; Jamaica, Haiti ..... 6. *S. gemmipara* C. Chr.
2b. Species of southeastern Brazil.
6a. Pinnae cut ½ or less to the costa; veins 3–7 per lobe.
7a. Pinnae entire to lobed less than ¼ to the costa ..... 8. *S. heterocarpa* (Fée) Rosenstock
7b. Pinnae lobed ⅓–½ to the costa.
8a. Sori inframedial; fertile pinnae 1.1–2.3 cm wide, the sinuses broad, U-shaped ..... 19. *S. prionites* (Kunze) C. Chr.
8b. Sori medial to supramedial; fertile pinnae 2.5–4 cm wide, the sinuses narrow, V-shaped ..... 23. *S. tyucana* (Raddi) C. Chr.
6b. Pinnae cut ½–⅞ to the costa; veins 5–15 per lobe.
9a. Pinnae cut ⅔–⅞ to the costa, the distal ones often with the basal basiscopic lobe adnate and ca. perpendicular to the rachis; (Fig. 10b); veins 9–15 per lobe .. 3. *S. caudata* (Raddi) C. Chr.
9b. Pinnae cut ½–⅔ to the costa, the distal ones lacking a basal basiscopic lobe adnate to the rachis; veins 5–8(–10) per lobe.
10a. Sinuses narrow, V-shaped ..... 1. *S. brevinervis* (Fée) R. C. Moran
10b. Sinuses broad, U-shaped ..... 24. *S. ulei* (Christ) Sehnem
1b. Key to all species (including those of the Antilles and southeastern Brazil).
11a. Veins anastomosing.
12a. Rachis and costae puberulent abaxially.
13a. Free pinna pairs 7–10; buds often present in the axils of the medial and distal pinnae (these best seen adaxially) ..... 2. *S. bulbifera* R. C. Moran
13b. Free pinna pairs 1–3(–4); buds absent or (in Ecuador) rarely present ..... 9. *S. heterophlebia* (Baker) R. C. Moran
12b. Rachis and costae lacking hairs abaxially.
14a. Petiole abaxially atropurpureous, lustrous ..... 12. *S. killipiana* Lellinger
14b. Petiole abaxially brown, tan, or stramineous, dull.
15a. Lamina thin, internal punctate glands easily visible (with magnification); sori round; areoles of sterile leaves with 1 or 2 irregular, curved or forked excurrent veinlets; western Venezuela, northern Colombia ..... 20. *S. pterorhachis* R. C. Moran
15b. Lamina thick, the internal punctate glands not visible (with magnification); sori round or oblong with a strong tendency to become arcuate; areoles of sterile leaves with 1 straight (or nearly so) excurrent veinlet (Fig. 24e); Ecuador, Peru ..... 17. *S. opaca* (Baker) C. Chr.
11b. Veins free or with a few casual anastomoses.
16a. Pinnae entire, crenate, or cut less than ¼ to the costa.
17a. Pinnae confluent in the distal ½–⅓ of the lamina by a conspicuous, long-decurrent wing (Fig. 21b) ..... 14. *S. longicaudata* (Liebm.) C. Chr.
17b. Pinnae confluent in the distal ¼–⅛ of the lamina, the bases short-decurrent.
18a. Pinna pairs 18–32; Lesser Antilles, Guianas, and eastern Venezuela ..... 21. *S. rotundata* (Willd.) C. Chr.
18b. Pinna pairs 12–17; southeastern Brazil ..... 8. *S. heterocarpa* (Fée) Rosenstock
16b. Pinnae cut ¼ to all the way to the costa.
19a. Pinnae confluent in the distal ½–⅓ of the lamina by a conspicuous, long-decurrent wing.
20a. Pinnae (4.5–)9–11 cm; leaves 0.3–0.7 m; sori paraphysate with multicellular, dark brown hairs ..... 15. *S. michaelis* (Baker) C. Chr.
20b. Pinnae 14–20 cm; leaves 0.8–1.4 m; sori not paraphysate or (in South America) with filiform scales among the sporangia ..... 14. *S. longicaudata* (Liebm.) C. Chr.
19b. Pinnae confluent in the distal ¼–⅛ of the lamina, the bases short-decurrent.
21a. Distal pinnae with the basiscopic basal lobe adnate and ca. perpendicular to the rachis (Figs. 10b, 14a), with the costule arising from the rachis.
22a. Pinnae 4–7 cm wide; lamina lacking buds; veins 9–15 per segment; southeastern Brazil ..... 3. *S. caudata* (Raddi) C. Chr.
22b. Pinnae 1.5–2.5 cm wide; lamina of small sterile leaves with buds in the axils

of the distal pinnae; veins 6–10 per segment; Cuba ..... 7. *S. hemiptera* (Maxon) C. Chr.

21b. Distal pinnae with the basal basiscopic lobe adnate to the costa or only partly adnate to the rachis, the costule arising from the costa.

23a. Lamina 2-pinnate-pinnatifid ..... 13. *S. lechleri* (Mett.) C. Chr.

23b. Lamina 1-pinnate-pinnatifid to nearly 2-pinnate.

24a. Costular scales bullate *or* buds present in the axils of the distal pinnae; Jamaica, Haiti.

25a. Pinnae 15–23 cm, pairs 22–26; lamina without buds in the axils of the distal pinnae; sori covered by an indusiumlike scale ..... 11. *S. jamaicensis* (Desv.) Proctor

25b. Pinnae (4–)9–14 cm, pairs 9–20; lamina with buds in the axils of the distal pinnae; sori not covered by an indusiumlike scale ..... 6. *S. gemmipara* C. Chr.

24a. Costular scales not bullate; buds absent in the axils of the distal pinnae; southern Mexico to southeastern Brazil.

26a. Bases of the medial pinnae overlapping the rachis (Figs. 12c, e, 23a); Costa Rica, Panama, northern Venezuela.

27a. Pinnae 3–6 cm wide, cut ¾ to nearly all the way to the costa; Costa Rica, Panama ... 5. *S. contracta* (Christ) C. Chr.

27b. Pinnae 2–3.5 cm wide, cut ¼–½ to the costa; northern Venezuela ..... 16. *S. nephrodioides* (Klotzsch) C. Chr.

26b. Bases of the medial pinnae not overlapping the rachis; southern Mexico to Bolivia, southeastern Brazil.

28a. Pinnae 8–12 cm; southern Mexico ..... 4. *S. chimalapensis* Mickel & Beitel

28b. Pinnae 12–40 cm.

29a. Pinnae 1.1–2.3 cm wide; veins 3–5 per lobe; southeastern Brazil. ..... 19. *S. prionites* (Kunze) C. Chr.

29b. Pinnae 2–6 cm wide; veins 4–14 per lobe.

30a. Pinnae cut ⅓–½ to the costa; southeastern Brazil ..... 23. *S. tyucana* (Raddi) C. Chr.

30b. Pinnae cut ½–⅔ to the costa.

31a. Sori subtended by an indusiumlike scale (Fig. 17b); western Ecuador ..... 10. *S. ichthiosma* (Sodiro) C. Chr.

31b. Sori lacking an indusiumlike scale.

32a. Scales of the costae and costules lanceolate to linear, mixed with smaller fibrillose ones; Colombia to Bolivia ..... 18. *S. pellucidopunctata* (C. Chr.) C. Chr.

32b. Scales of the costae and costules ovate to lanceolate, filiform scales absent.

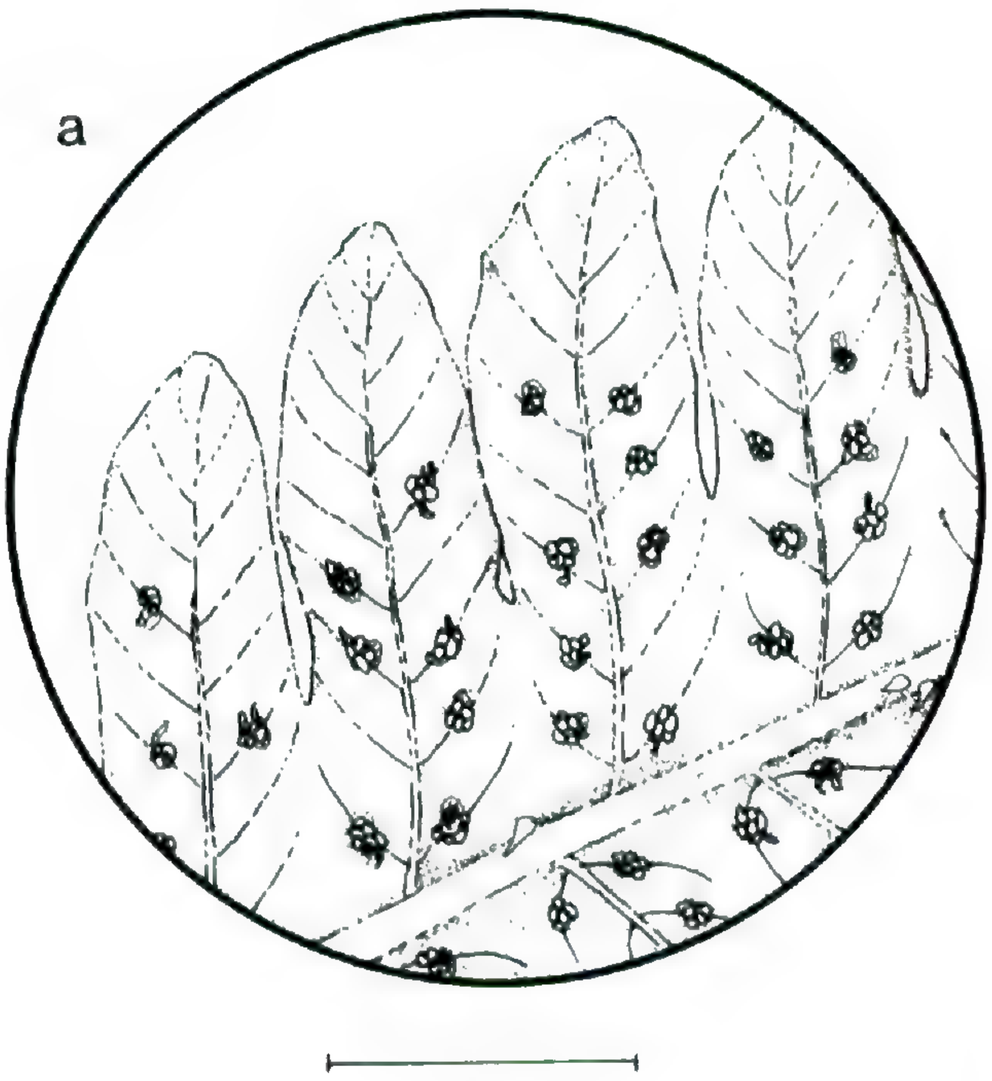
33a. Sori medial; southern Mexico to Ecuador ..... 22. *S. sordida* (Maxon) C. Chr.

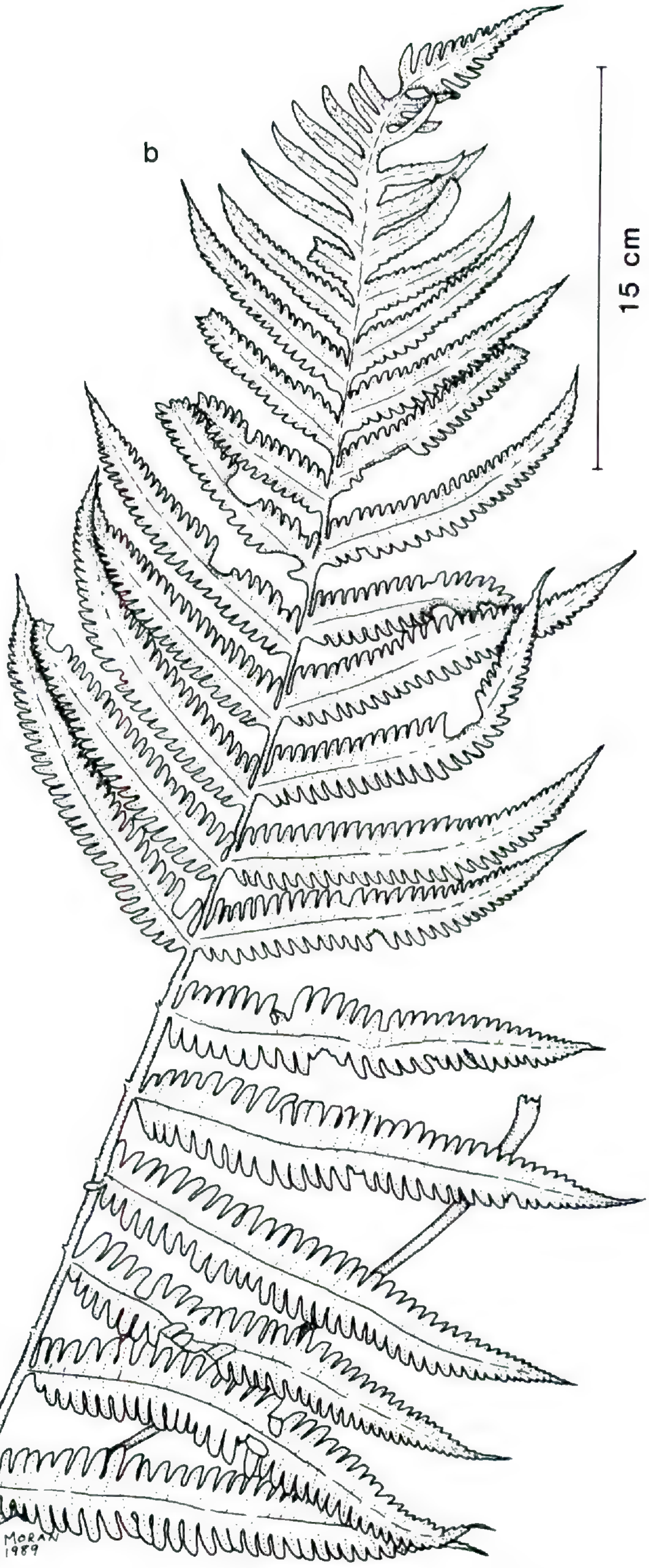
33b. Sori inframedial; southeastern Brazil.

34a. Sinuses narrow, V-shaped ..... 1. *S. brevinervis* (Fée) R. C. Moran

34b. Sinuses broad, U-shaped ..... 24. *S. ulei* (C. Chr.) Sehnem

1. Stigmatopteris brevinervis (Fée) R. C. Moran, comb. nov. *Phegopteris brevinervis* Fée, Crypt. Vasc. Brésil 1: 243, t. 77, fig. 2. 1869. SYNTYPES: Brazil. Rio de Janeiro: Organ Mountains, June 1869, *Glaziou 3333* pro parte (lectotype, here designated, P); Organ Mountains, *Glaziou 2400* pro parte (P). Figure 8. Map 1.





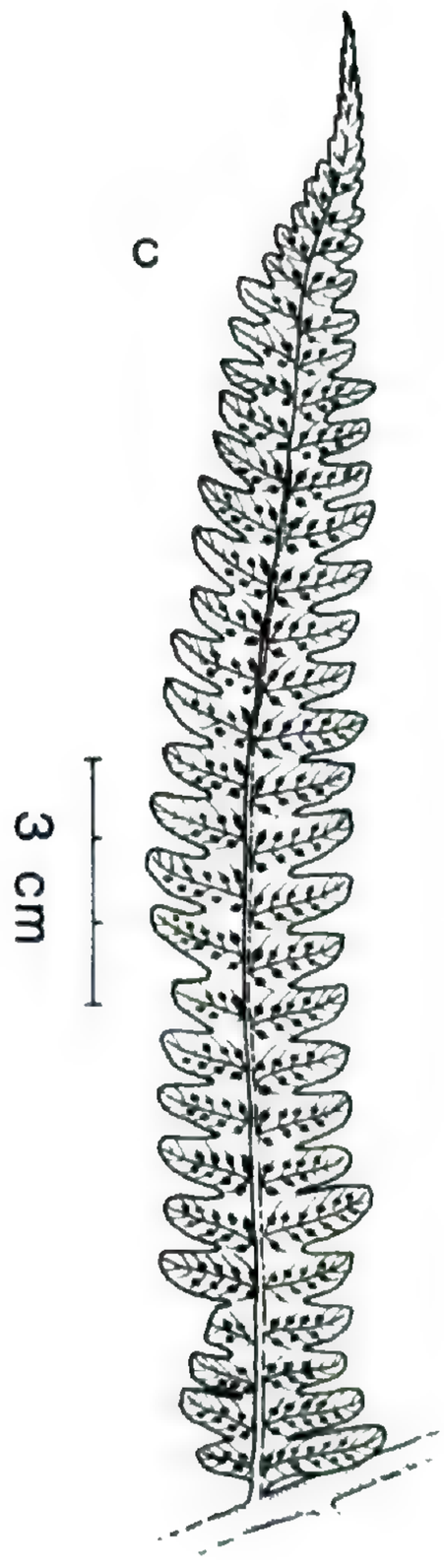
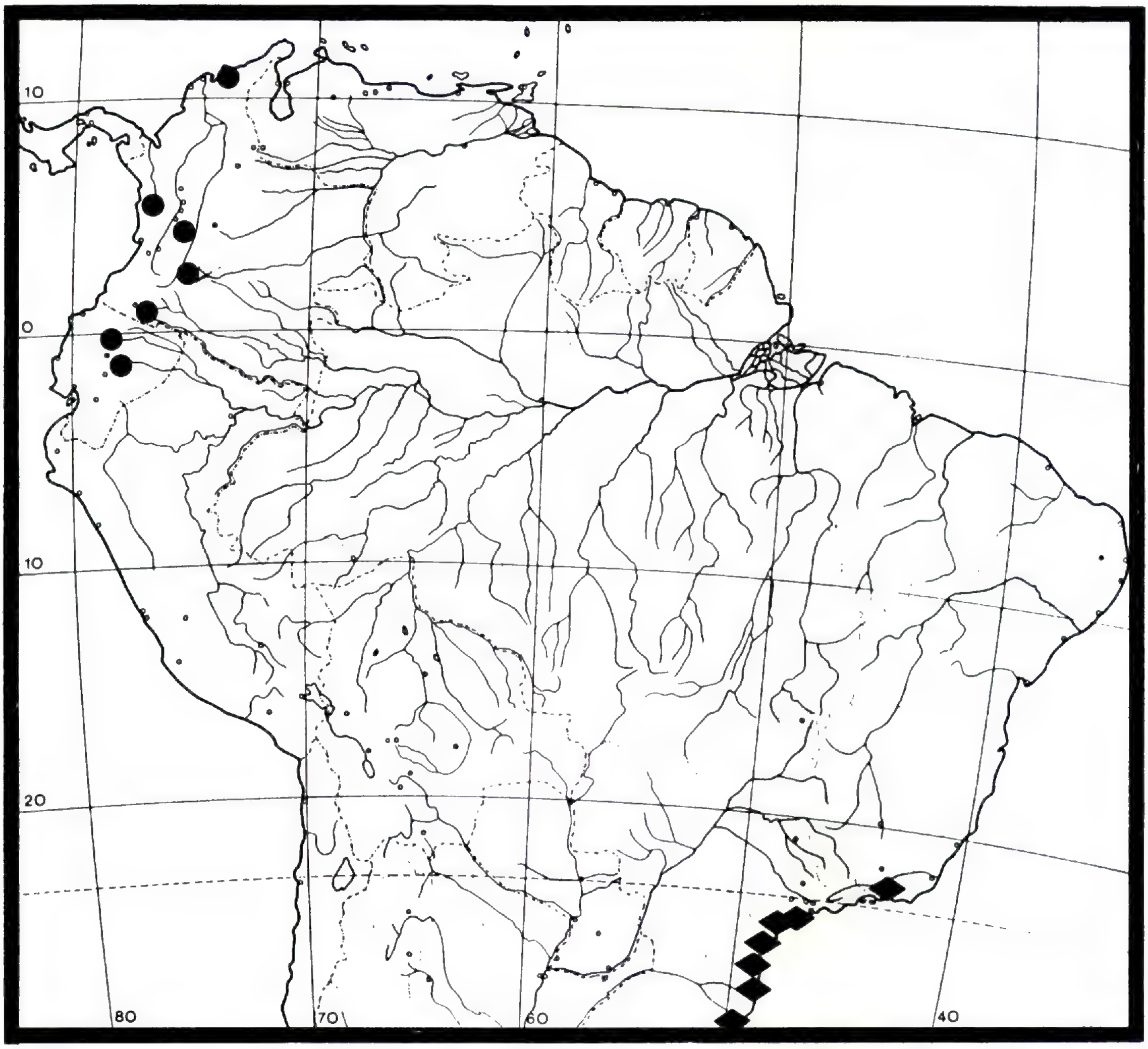


FIGURE 8. *Stigmatopteris brevinervis*.—a. Abaxial surface of a pinna (*Brade 8250*, UC).—b. Leaf (*Dusén 725a*, distal half, NY; proximal half, MO).—c. Fertile pinna (*Glaziou 2400*, P).



MAP 1. Distribution of *Stigmatopteris bulbifera* (dots) and *S. brevinervis* (diamonds).

Stigmatopteris bradei Rosenstock, Repert. Spec. Nov. Regni Veg. 21: 347. 1925. TYPE: Brazil. São Paulo: município Iguape, Serrinha, *Brade 8250* (holotype, S? not seen; isotypes, PH, UC).

Rhizome short-creeping; leaves to 1.5 m; petiole ca. equaling the lamina, stramineous to brown, scaly at the base, the scales 5–12 × 1–2 mm, brown, thin, lanceolate; lamina 1-pinnate-pinnatifid, lanceolate, lacking bulblets, only a few distalmost pinnae with short-decurrent bases; pinnae 16–24 × 2.3–4 cm, 15–20 pairs, cut ½–⅔ to the costa, the base sessile or nearly so, the basal pinnae short-stalked; segments 5–6.5 mm wide, separated by narrow, V-shaped sinuses, entire to denticulate at the apex; rachis and costae stramineous or occasionally the rachis tan, sparsely scaly, the scales ovate to lanceolate; veins free, not forked, 5–8(–10) per lobe; sori inframedial; indusial scale absent.

Additional specimens examined. BRAZIL. MINAS GERAIS: Serra de Babilonia (Minas), 6 Apr. 1868, *Glaziou 2400* (P). PARANÁ: Serra do Mar, Volta Grande, 400 m, *Dusén 725a* (BM, GH, MO); Guaratuba, *Dusén 13727* (GH). RIO DE JANEIRO: Organ Mountains, 29 May 1869, *Glaziou 3333* (P). SANTA CATARINA: Meleiro, Araranguá, *Reitz C 206* (US); Itacorubí, Florianópolis, *Reitz 276* (US); Morro da Lagoa, *Rohr 353* (US). SÃO PAULO: município Iguape, Peroupara, *Brade 8250* (PH, UC); município Iguape, Serrinha, *Brade 8343* (US). STATE UNKNOWN: no locality, *Müller 1038* (US).

Stigmatopteris brevinervis is endemic to the coastal mountains of southeastern Brazil (Map 1); the only recorded elevation is 400 m. It closely resembles *S. tyucana*, the only difference being the degree of cutting. In *S. tyucana*, the pinnae are cut ¼–½ to the costa; in *S. brevinervis*, the pinnae are cut ½–⅔ to the costa. *Stigmatopteris brevinervis* has a larger leaf and more pinnae than does *S. tyucana*, which suggests that *S. brevinervis*

may be merely a larger, more deeply cut form. Another difference is that *most* specimens of *S. tyucana* have medial to supramedial sori, whereas all those of *S. brevinervis* have inframedial sori. These two species are very similar and perhaps future study will show that they are conspecific.

2. Stigmatopteris bulbifera R. C. Moran, sp. nov. TYPE: Ecuador. Napo: Cerro Huacamoyos, on road Baeza–Tena, ca. 34 km from Baeza, 2,000 m, *Øllgaard et al. 35866* (holotype, AAU, 5 sheets). Figure 9. Map 1.

Folia 1-pinnata, pinnis 7–10 utroque costae latere, gemmis praesentibus in axillis pinnarum distalium; rhachis et costae abaxialiter glanduloso-pubescentes; venae irregulariter anastomosantes.

Rhizome short-creeping, the internodes 0.5–2 cm, the apex scaly, the scales 1–4 mm, lanceolate, dark brown, entire; leaves to 0.9–1.3 m; petioles nearly equaling the lamina, dull, brown, scaly, the scales 5–10 mm, lanceolate, brown, entire, not shiny adaxially; lamina 1-pinnate, oblong-deltate, buds usually present in the axils of the distal or medial pinnae; free pinna pairs 7–10; basal pinnae not reduced, widest near the middle, stalked, the stalk 2–5 mm; medial pinnae 18–25(–35) × 2.5–4.5(–6) cm, widest near the middle, the margins crenate-serrate or, in large leaves, cut ⅛ to the costa; rachis and costae tan, puberulent and scaly, the hairs less than 0.1 mm, erect, capitate-glandular; veins partly free and partly anastomosing; sori discrete, round, lacking an indusial scale.

Additional specimens examined. COLOMBIA. CAQUETA: Putumayo, cerca de Buenosaires, 2,060 m, *Hageman & Leist 2072* (COL). CHOCÓ: between Pueblo Rico (Risaralda) and Istmina (Chocó), along Quebrada Antón, 15 km W of Santa Cecilia, 240 m, *Croat 70911* (MO, UC). HUILA: Cordillera Oriental, Caquetá side of Huila–Caquetá divide, 20 km SE of Garzón, 2,380 m, *Little 9380* (COL, GH, US). MAGDALENA: Sierra Nevada de Santa Marta, finca Los Arroyitos, 1,600–1,700 m, *Kirkbride 2377* (COL). QUINDÍO: "Quindío" *Triana 615* (COL). ECUADOR. PICHINCHA: Saloya, road to Las Palmeras, mountain left of road across from Las Lagñas, 1,850 m, *Heinrichs 550* (F, Z).

Stigmatopteris bulbifera occurs in Colombia and Ecuador (Map 1), where it grows in wet forests from (240–)1,600 to 2,380 m. It resembles *S. heterophlebia* in that both are 1-pinnate, have anastomosing veins, and are beset with numerous capitate-glandular hairs on the abaxial surface of the axes. The two species are easily distinguished, however, by the characteristics given in the key. Other less constant characteristics are that *S. bulbifera* tends to be a much larger plant, with leaves over one meter tall, and that *S. bulbifera* grows at higher elevations than *S. heterophlebia*. In general, *S. bulbifera* has a greater number of free veinlets per pinnae, sometimes up to 90% free. The buds are best seen on the adaxial side of the leaf.

3. Stigmatopteris caudata (Raddi) C. Chr., Bot. Tidsskr. 29: 302. 1909. *Polypodium caudatum* Raddi, Opusc. Sci. 3: 288. 1819. *Dryopteris caudata* (Raddi) C. Chr., Index Filic. 257. 1905. TYPE: Brazil. Rio de Janeiro: Gávea, Tijucas, *Raddi s.n.* (holotype, FI or PI not seen). Figure 10. Map. 2.

Polypodium caudatum Kaulf., Enum. Filic. 113. 1824. TYPE: Brazil. Rio de Janeiro: *Mertens s.n.* (holotype, LZ—destroyed; isotype, C not seen; photos F, GH ex C).

Rhizome short-creeping; leaves to 2 m long; petiole ½ to equaling the length of the lamina, brown, scaly, the scales 3–8 × 1–2.5 mm, lanceolate, brown, thin, lacking fibrillose scales; lamina 1-pinnate-pinnatisect, lanceolate, lacking buds, glands obscure; pinnae 15–32 × 4–7 cm, 15–20 pairs, cut ⅔–⅞ to the costa, sessile, the distal ones adnate with the basal basiscopic lobe adnate to the rachis; lobes 3–8 cm wide, separated by broad, open, U-shaped sinuses, serrate on all sides, occasionally lobed, the basal basiscopic segments reduced; rachis and costae tan to brown, scaly, the scales nonbullate, ovate, lanceolate; veins free, 9–15 per lobe, unbranched or 1-forked with a short acroscopic branch which (in fertile segments) bears the sorus; sori lacking an indusiumlike scale.

Additional specimens examined. BRAZIL. ESPÍRITO SANTO: Jatiboca, *Brade 18228* (NY). PARANÁ: município de Morretes, base do morro 7-astrada Graciosa, 1 m, *Dombrowski & Saito 1232* (US); Desvio Ypiranga, *Dusén 10341* (B, BM, US); Antonina, opp. Rio Demora, 200 m, *Dusén 14687* (BM, F, G, NY, US, Z); Serra do Mar, 580 m, *Jansson 740a* (F, G); município Paranaguá, Pico Torto, encosta oriental, 300 m, *Hatschbach 22873* (L, UC); município Morretes, Estr. Graciosa, Greta Funda, 500 m, *Hatschbach 24739* (NY, UC); município Guaraqueçaba, Rio do Custa, 50 m, *Hatschbach & Scherer 26665* (UC). RIO DE JANEIRO: Petropolis "Independencia," *Alston & Lutz 289* (BM); Nouvelle Fribourg, *Claussen 133* (G, P); Palmeiras, *Preston s.n.* (K); Mt. Corcovado, 1815, *Cunningham s.n.* (BM, NY); Rio Corcovado, *Dusén 2538* (MO); Organ Mts., 1837, *Gardner 131* (K); Rio de Janeiro, 1822, *Gaudichaud s.n.* (B, F, G, K, P); Rio de Janeiro, *Glaziou 2396* (P), *6414* (B, P); Sebastianopol, *Martius s.n.* (B); alto Macahé, *Mendonca 1355* (B); Rio de Janeiro, *Miers s.n.* (B, BM, K, P); Rio de Janeiro, *Mosén 2694* (B); Rio de Janeiro, 1840, *Regnell 254a* (GH, NY, P); 1841, *Regnell 358* (US); near Rio de Janeiro, *Sello s.n.* (B, BM); brook trail between Paineiras and Jardim Botanico, 100–400 m, *L. B. Smith*

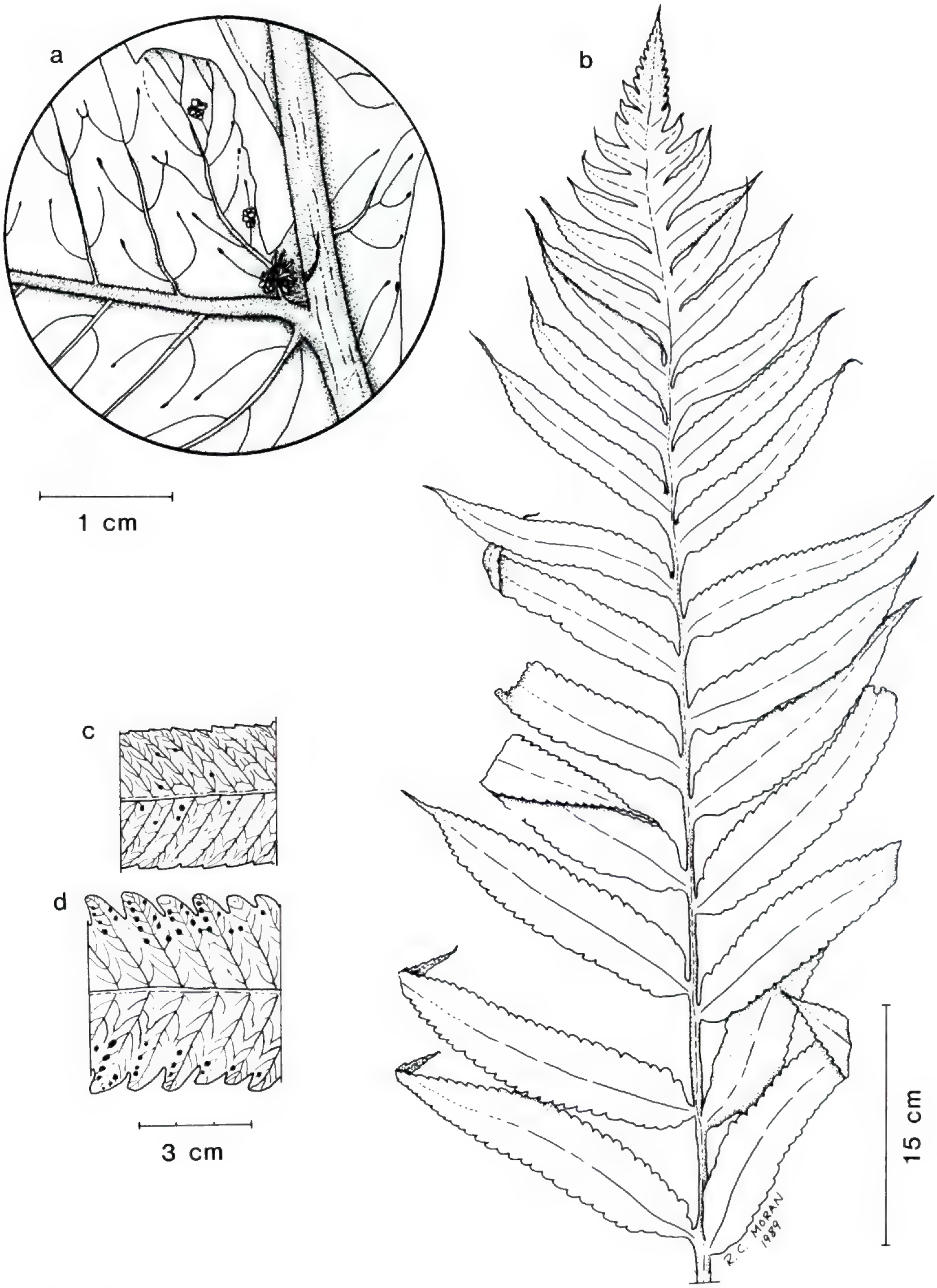


FIGURE 9. *Stigmatopteris bulbifera*.—a. Juncture of rachis and costa with bud (*Øllgaard et al. 35866*, AAU).—b. Lamina (*Heinrichs 550*, distal half, B; proximal half, F).—c. Part of fertile pinna (*Hageman & Leist 2072*, COL).—d. Part of fertile pinna (*Øllgaard et al. 35866*, AAU).

1391 (GH); near Rio de Janeiro, *U.S. Exploring Expedition 23* (US); near Rio de Janeiro and Bahia, *Webb s.n.* (MICH, NY, US). SANTA CATARINA: município de Sombrio, Retiro, Araranguá, *Reitz 227* (US); município de Meleiro, Araranguá, perto da cidade, *Reitz C205* (US); município de Brusque, Morro de Bateia, 100 m, *Reitz 1909* (BM); município de Brusque, Ribeirão do Ouro, 600 m, *Reitz 3542* (US); município de Ibirama, Horto Florestal I.N.P., 400 m, *Reitz & Klein 3077* (US); município de Florianópolis, Sertão da Lagoa, *Rohr 1072* (B, L, NY,

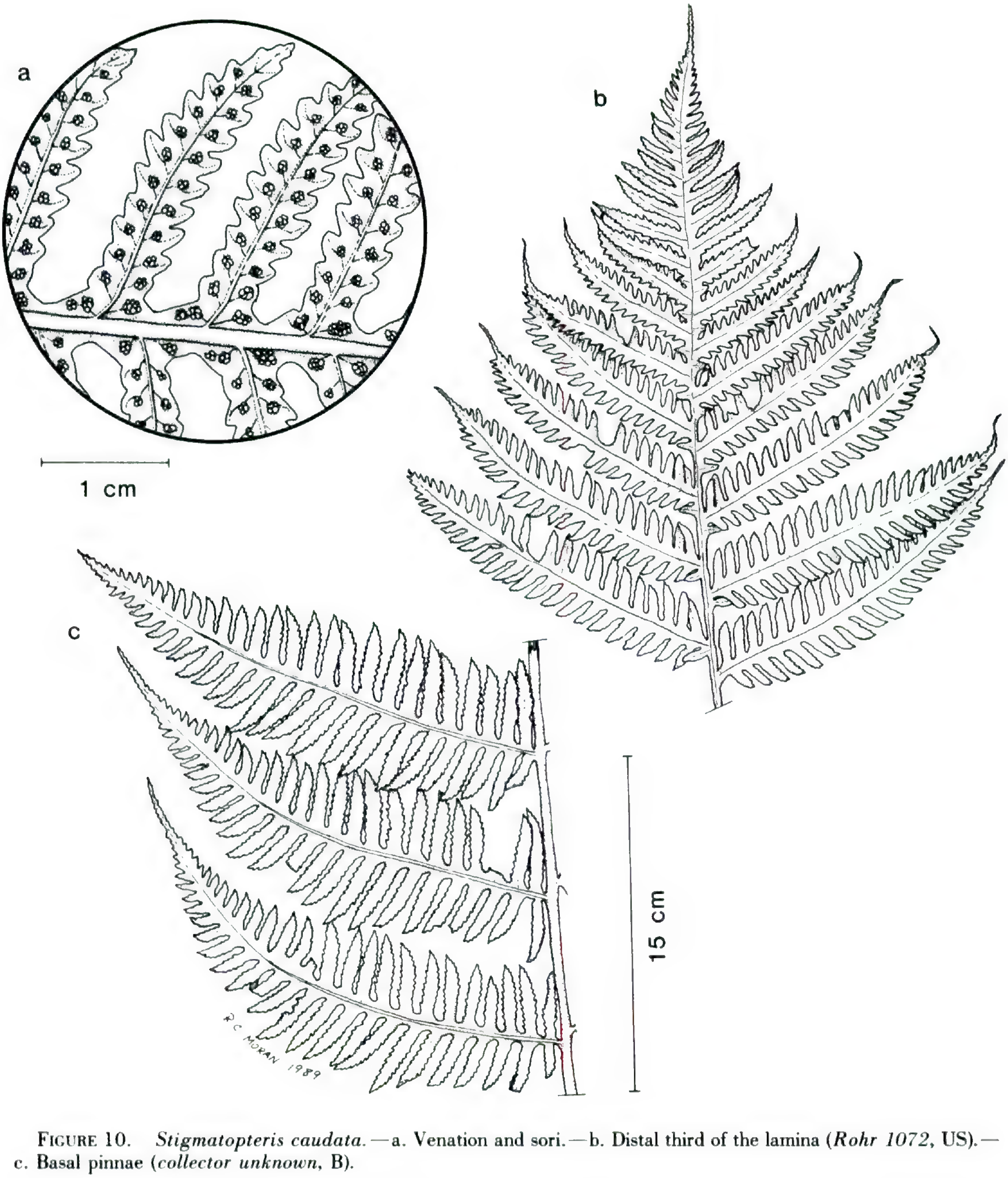
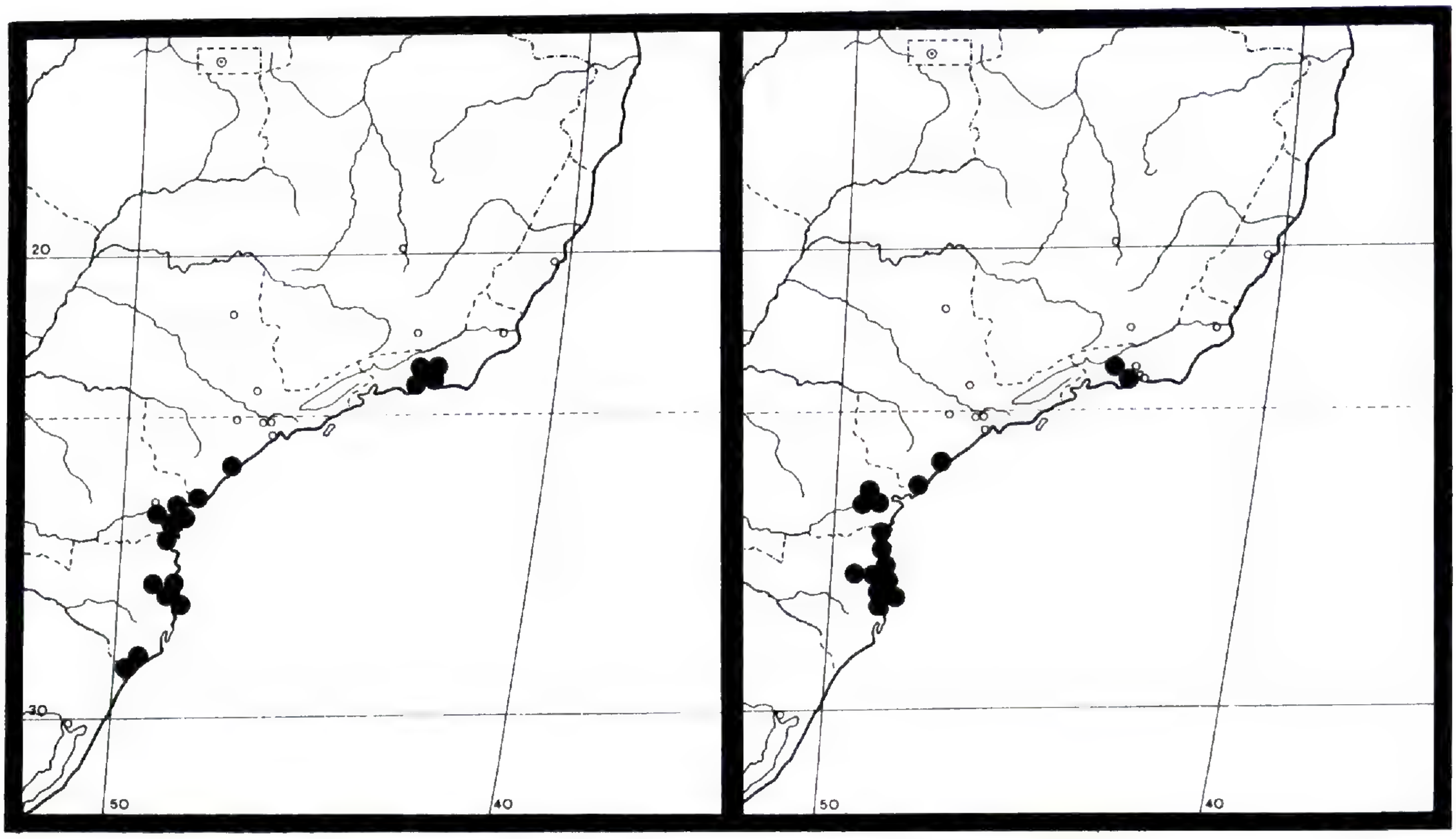


FIGURE 10. *Stigmatopteris caudata*.—a. Venation and sori.—b. Distal third of the lamina (*Rohr 1072*, US).—c. Basal pinnae (*collector unknown*, B).

US); município de Joinville, *Schmalz 191* (F); Peninsula da Gloria, Feb. 1884, *Ule 68* (K), *70* (P). SÃO PAULO: Iguape, Apr. 1922, *Brade s.n.* (US); Peroupara, *Brade 8478* (NY, UC); Serra do Mar, *Luederwaldt 21821* (GH); no locality, 1906, *Wacket s.n.* [Rosenstock, *Filices austrobrasilienses* no. 286] (B, GH, P, UC).

Stigmatopteris caudata is endemic to southeastern Brazil (Map 2) where it grows in wet forests from 0 to 600 m. It is the most highly cut species of *Stigmatopteris* in southeastern Brazil and has characteristic serrate segments separated by broad, U-shaped sinuses (Fig. 10a). In its size and cutting, this species resembles *S. ichthiosma*, an Ecuadorian species, but differs by its more deeply serrate or lobed segments, wider sinuses, generally wider pinnae, and lack of an indusiumlike scale. The petiole scales also differ between the two species: *S. caudata* has thin scales, whereas at least some of those on *S. ichthiosma* are darkly sclerified adaxially.

Although I have not seen the type specimen of this species, I feel confident on the basis of Raddi's



MAP 2. Distribution of *Stigmatopteris caudata* (left) and *S. heterocarpa* (right).

original description and his later illustration (Raddi, 1825, fig. 39) that the name is here applied correctly.

4. Stigmatopteris chimalapensis Mickel & Beitel, Mem. New York Bot. Gard. 46: 356, fig. 129E, F. 1988. TYPE: Mexico. Oaxaca: Municipio Santa María Chimalapa, Cañada E de la vereda a La Gloria, ca. 8 km SE de Santa María, 350 m, *Hernández 1282* (holotype, NY). Figure 11.

Rhizome erect, short; leaf 70 cm; petiole equaling the lamina, brown to stramineous, sparsely scaly, the scales 1–3 mm, ovate to lanceolate, entire, appressed, shiny black abaxially; lamina 1-pinnate-pinnatifid, lanceolate, bulblets lacking; basal pinnae equilateral, widest at or slightly above the middle, short-stalked, the stalk 2 mm; medial pinnae 8–12 × 1.3–2 cm, equilateral, widest at the base, cut ca. ½ or slightly less to the costae, 14 pairs, sessile; lobes entire or slightly serrate at the apex, the proximal acroscopic ones elongated; rachis brown, costae stramineous, both axes scaly, the scales irregularly ovate to lanceolate, the margins ciliate; veins free, unbranched, 4–6 per lobe; sori lacking an indusial scale.

This species is known only from the type collection. It resembles *S. sordida*, with which it may eventually prove conspecific, but differs by its smaller size and less-cut pinnae.

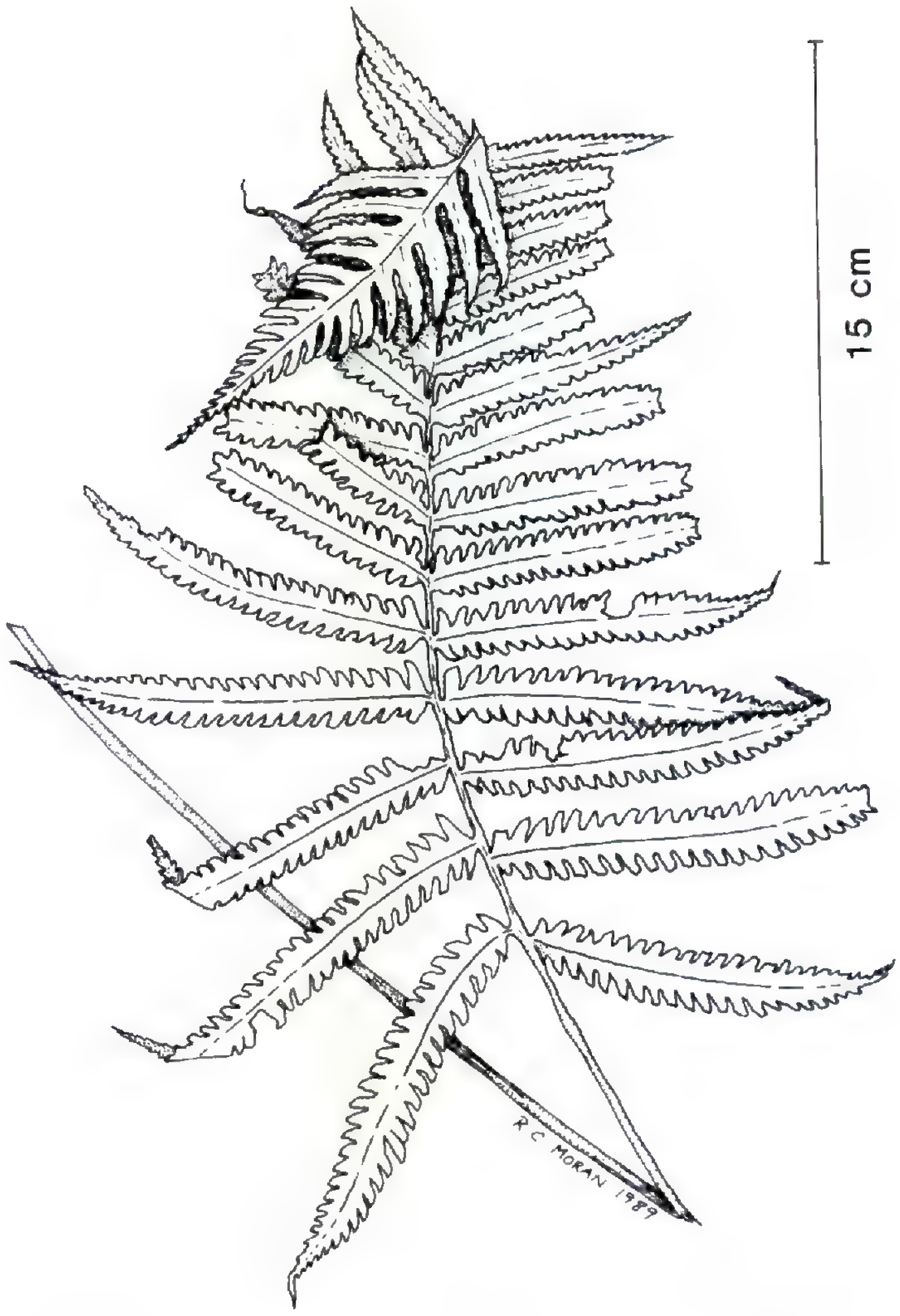


FIGURE 11. *Stigmatopteris chimalapensis.*—Leaf (*Hernández 1282*, NY).

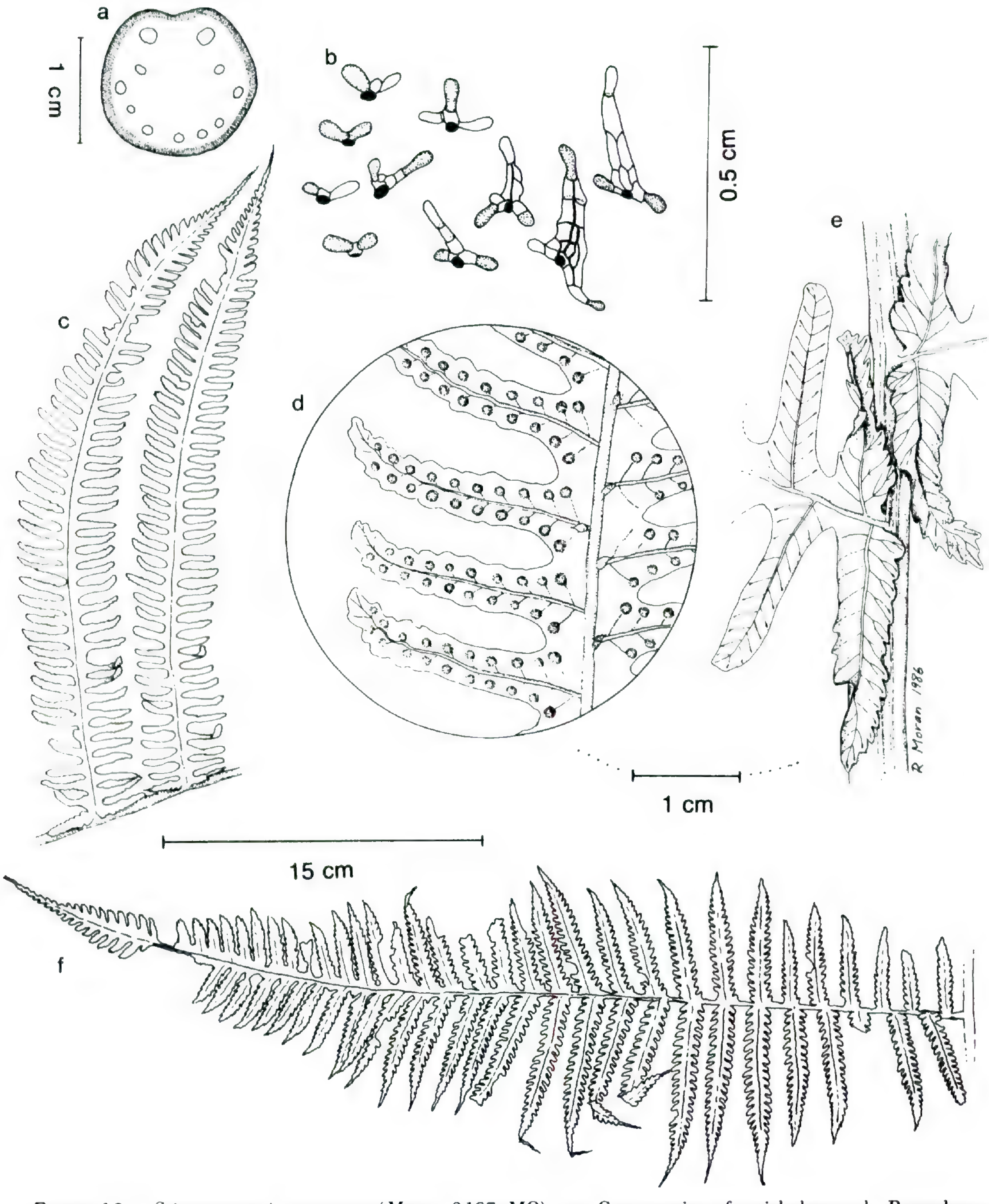


FIGURE 12. *Stigmatopteris contracta* (*Moran 3187*, MO).—a. Cross section of petiole base.—b. Proscales or microscales (uniseriate) and multiseriate scales from the distal portions of the abaxial surface of the lamina.—c. Medial pinnae.—d. Venation and sori.—e. Segments of the pinna bases overlapping the rachis.—f. Large basal pinna.

5. Stigmatopteris contracta (Christ) C. Chr., Bot. Tidsskr. 29: 304. 1909. *Aspidium caudatum* var. *contractum* Christ, Bull. Herb. Boissier sér. 2, 6: 162. 1906. SYNTYPES: Costa Rica. Cartago: Navarro, 1905, 1,100 m, *Wercklé s.n.* (lectotype, here designated, P; isolectotypes, BM, MICH, NY, US; photos, GH, NY ex BM); Colombia (Nouvelle Granada), *Schlim 1683* (P—herb. Christ?, BM). (This specimen is here referred to *S. pellucidopunctata*.) Figure 12.

Rhizome up to 10 cm, erect or ascending; leaves 1–3 m; petiole ½–¾ the length of the lamina,

brown, the scales 1–3 mm, ovate to nearly circular, opaque, appressed, dull brown adaxially, shiny black abaxially, these sometimes mixed with larger, thin, translucent, flaccid scales; lamina 80–200 × 40–95 cm, 1-pinnate-pinnatifid, lanceolate, bulblets lacking; medial pinnae 20–35 × 3–6 cm, linear, cut ¾ to nearly all the way to the costae, pairs 20–26, the base overlapping the rachis; basal pinnae 7–15 cm wide, elongated basiscopically, widest near the middle where the basiscopic basal segments are twice as long as the acroscopic ones; segments entire to crenate or serrate, the fertile ones contracted, their sinuses 1–2 times the width of the segments, U-shaped, the basal segments on both sides prolonged and overlapping the rachis; rachis brown; costae stramineous, scaly, the scales 1–2 mm, few, scattered, ovate, entire or nearly so, never fibrillose; veins free, 8–18 in the medial segments of the medial pinnae, those of the fertile segments unbranched, those of the sterile segments branched or unbranched; sori with indusial scale absent or rarely present, the scale ovate-lanceolate, borne on the basiscopic side, stipitate and held above the sporangia.

Additional specimens examined. COSTA RICA. ALAJUELA: canyon of Río Cariblanco and W slope and summit of ridge between Río Cariblanco and Quebrada Quicuyal, SW of Cariblanco, 840–950 m, *A. R. Smith et al. 1862* (MO, NY, UC); Monteverde Cloud Forest Reserve, 1,250–1,350 m, *Burger et al. 10735* (CR, F, NY, US); along road from San Ramón to Bajo Rodríguez, at Río Cataratas, *Croat 68108* (MO, UC); Monte Verde Reserve, E slope of Cerro Centinelas, vicinity of Finca Peña Blanca, 1,300–1,400 m, *Grayum 5374* (MO, UC, US); Univ. of San Ramón's Biological Field Station, 1,100 m, *Moran 3187* (F, MO), *4126* (CR); N slope of ridge along quebrada draining E to Río Cataratitas, ca. 20 km NW of San Ramón, 850 m, *A. R. Smith et al. 2247* (CR, MO, UC); Reserva Forestal de San Ramón, Río San Lorenzito, 800–1,000 m, *Herrera et al. 336*, (MO, UC). CARTAGO: Pejivalle, *Lancaster 836* (BM); El Muñeco, 1,400–1,500 m, *Standley & Torres R. 51061* (US), *Stork 2658* (UC, US); Navarro, 1,500 m, *Torres 49* (US); without locality, *Endress s.n.* (K); 10 km SW of Navarro on a winding trail ca. 10 km S of Cartago and 1 km S of Finca Montecristo, 1,400–1,600 m, *White & Lucansky 1968150* (DUKE, GH); Reserva de Tapantí, *Gómez 1133* (CR), *2330* (CR, F, GH, MO, NY, US), *18905* (AAU, CR, MO, UC); forest near the entrance to Parque Nacional Tapantí, 1,270 m, *Moran 3330* (CR, F, GH, MO, NY); along tributary of Quebrada Casa Blanca Tapantí, 1,350 m, *Grayum & Sleeper 3714* (CR, MO, UC); slope N of Quebrada Casa Blanca, Tapantí, 1,350 m, *Grayum 4570* (MO); ca. 22 km E of Turrialba, high ridge above Plantanillo, 1,200–1,450 m, *Mickel 3430* (NY, UC, US); Turrialba, *Rojas G. s.n.* (CR); Platanillo, 650–900 m, *de la Sota 5238* (US), *White & Lucansky 1968174* (DUKE). HEREDIA: Virgen del Socorro, 1,000 m, *Moran 3166* (MO), 1,500 m, *Wagner & Gómez 79027* (CR); Cinchona, above the Upper Sarapaquí Valley, ca. 1,200 m, *Scamman s.n.* (GH). LIMÓN: Siquirres, *Stork 2263* (MICH). SAN RAMÓN: La Hondura, 1,000 m, *Nisman S. 98* (GH), *Gómez 281* (CR), 1,300–1,700 m, *Standley 37834* (US); vicinity of La Hondura, 4 km S to 1 km N on Rte. 220, between Volcán Irazú and Volcán Barba, 1,250–1,500 m, *Mickel 2241* (NY), *2249* (NY, UC, US). PANAMA. CHIRIQUÍ: Boquete, Dexter Trail, *Cornman 1091* (F, GH, MICH, MO, UC); vicinity of El Boquete, 1,000–1,500 m, *Cornman 914* (US); valley of the Río Piarnasta, ca. 5 mi. E of Boquete, 1,600 m, *Killip 5159* (GH, MICH, MO, UC, US).

Stigmatopteris contracta grows from 650 to 1,600 m in the montane forests of Costa Rica and Panama. With leaves 1–3 m long, *S. contracta* is the largest species in the genus. The segments of the sterile and fertile leaves are subdimorphic, differing in width, cutting, and venation. The name *contracta* refers to the fertile segments, which are narrower than the sterile ones.

This species might be confused with large plants of *S. sordida*, which also grows in Costa Rica and Panama. *Stigmatopteris contracta* can be distinguished by its pinna bases that overlap the rachis, costal scales that are ovate and nearly entire, fertile segments that are contracted, and wide sinuses that are one to two times the width of the segments. A scalelike indusium is present on the type but absent from the other specimens.

I chose *Wercklé s.n.* as the lectotype because it preserves the previous usage of the species name, and it is more widely distributed in herbaria. The other syntype cited by Christ, *Schlim 1683*, is here referred to *S. pellucidopunctata*.

6. Stigmatopteris gemmipara C. Chr., Kongl. Svenska Vetenskapsakad. Handl. ser. 3, 16: 36, t. 9, figs. 5–7. 1937. *Dryopteris gemmipara* (C. Chr.) Maxon ex Proctor, Bull. Inst. Jamaica, Sci. Ser. 5: 26. 1953. TYPE: Haiti. Hotte, western group, stony ridge above La Mare Proux, near Torbec, 6 Dec. 1925, *Ekman 5268* (holotype, S? not seen; isotype, IJ not seen). Figure 13.

Rhizome erect to decumbent, compact; leaves to 1 m; petioles equaling the length of the lamina, brown, scaly, the scales 0.5–1 cm, linear-lanceolate, brown, a few black, sclerotic, opaque; lamina 1-pinnate-pinnatifid, narrowly elongate-triangular to lanceolate, with buds in axils of distal pinnae, the apex attenuate; pinnae (4–)9–14 × (1.5–)2.5–3.5(–4) cm, 9–20 pairs, widest at or near the base, cut ½ or more to the costa, the basal basiscopic segment occasionally free, reduced, the base of the proximal pinnae stalked, the stalk 4–6 mm; segments 4–6 mm wide at the middle, serrate, the apex obtuse, the basal basiscopic segment not ad-

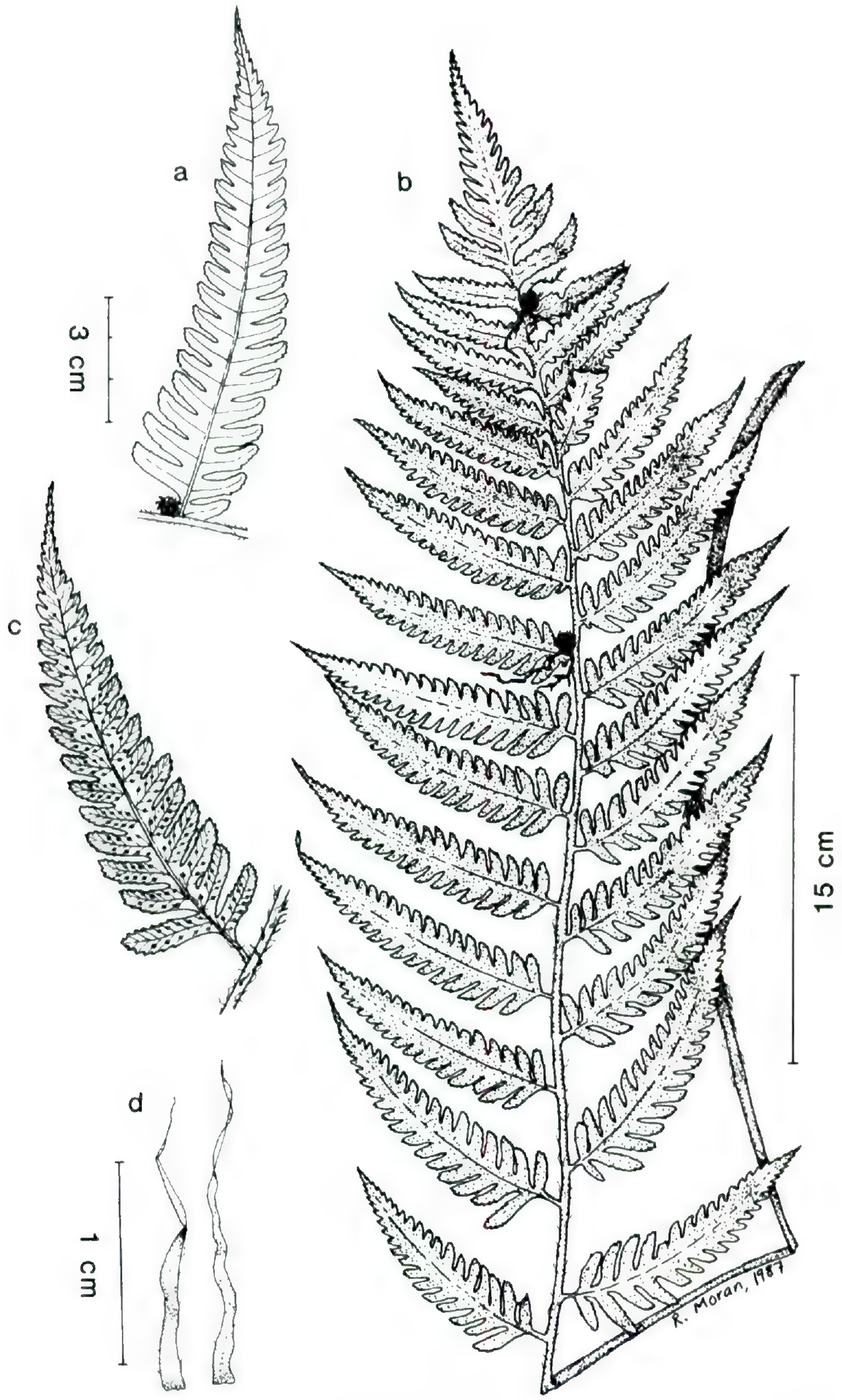


FIGURE 13. *Stigmatopteris gemmipara* (*Ekman 10113*, US).—a. Pinna with bud in axil.—b. Leaf with buds.—c. Fertile pinna, second from the base of b.—d. Petiole scales.

nate to the rachis; rachis and costae stramineous to light brown, scaly, the scales 2–3 mm, lanceolate to filiform, nonbullate, spreading, conspicuous, the costular scales nonbullate; veins free, mostly unbranched, 5–7(–8) per segment; sori lacking an indusiumlike scale.

Additional specimens examined. JAMAICA. PORTLAND: ca. 5 mi. SW of Priestman's River on the E slope of John Crow Mts., ca. 500 m, *Proctor 4257* (US). HAITI. Massif de la Hotte, western group, Torbec, Morne Formon, *Ekman 7424* (BM, G, K, US); Massif de la Hotte, Les Roseaux, hab. Quillaud, 1,000 m, *Ekman 10113* (US).

Stigmatopteris gemmipara grows only in Jamaica and Haiti in woods over limestone soils from 500 to 1,200 m. This species could be confused

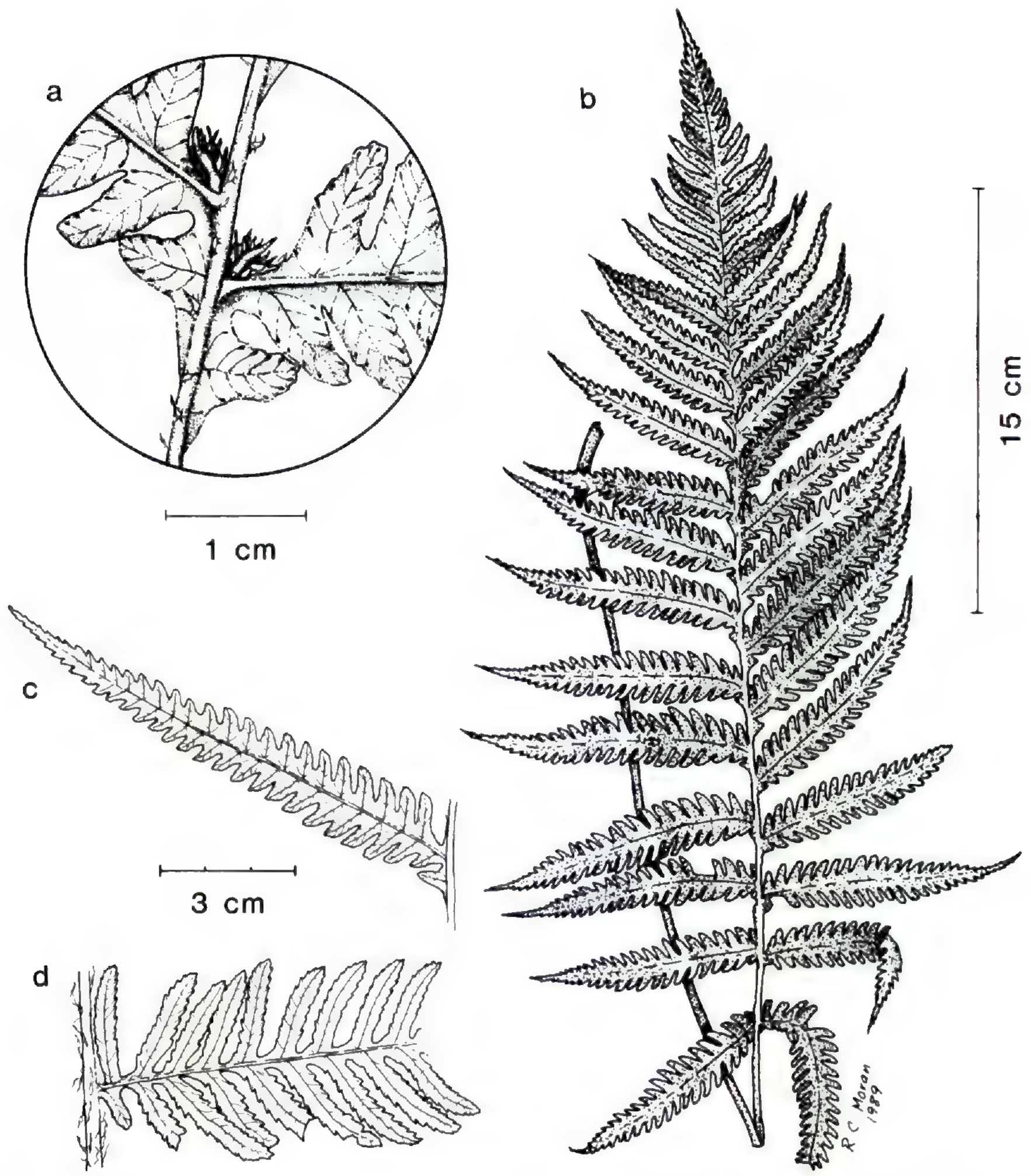


FIGURE 14. *Stigmatopteris hemiptera*.—a. Buds in the axils of distal pinnae; note that the basal basiscopic lobe is adnate to the rachis rather than to the costa (*León et al. 10409*, NY).—b. Leaf (*Ekman 14356*, GH).—c. Distal pinna (*Ekman 14356*, GH).—d. Proximal part of a large basal pinna (*Wright 1053*, US).

with *S. jamaicensis*, which is endemic to Jamaica, but that species lacks bulblets and has an indusiumlike scale subtending the sorus.

7. **Stigmatopteris hemiptera** (Maxon) C. Chr., Index Filic. Suppl. 3: 174. 1934. *Dryopteris hemiptera* Maxon, Contr. U.S. Natl. Herb. 24: 59. 1934. TYPE: Cuba, Sep. 1859–Jan. 1860, *Wright 1053* (holotype, US; isotypes, BM, G, GH, K, MO, fragment B, US). Figure 14.

Rhizome decumbent, compact; leaves 45–130 cm long; petioles ½ to equaling the lamina, stramineous to dull brown, sparsely scaly, the scales narrowly triangular, translucent or nearly so, not black and opaque; lamina 1-pinnate-pinnatifid, lanceolate, buds produced on small sterile leaves in the axils of the distal pinnae, the apex evenly tapered; pinnae 11–18 × 1.5–2.5 cm, 15–20 free pairs, widest below the middle, cut ½–⅞ to the costa, large plants occasionally with a free basal acroscopic pinnule, the base adnate in the distal ½ of the lamina, with the basal basiscopic lobe arising from the rachis rather than the costa; segments 3–4 mm wide, the margins serrate, the apex rounded; rachis and costae stramineous, scaly, the scales scattered, nonbullate; veins 6–10 per segment, mostly unbranched; glands not easily visible; sori nonparaphysate, lacking an indusiumlike scale.

Additional specimens examined. CUBA. ORIENTE: Sierra Maestra, Loma del Gato, *Clement 961* (GH, P, UC, US), 1,000 m, *1602* (Z); *Hioram & Clement 6442* (GH, US); Sierra Maestra, on the divide below Río Yara and Río Palmamocha, ca. 1,000 m, *Ekman 14356* (G, GH, NY, US); S side of the crest of the Sierra Maestra W of Aserraldero San Antonio de los Cumbres, region of La Bayamesa, 1,400–1,500 m, *Morton 9569* (US); Loma

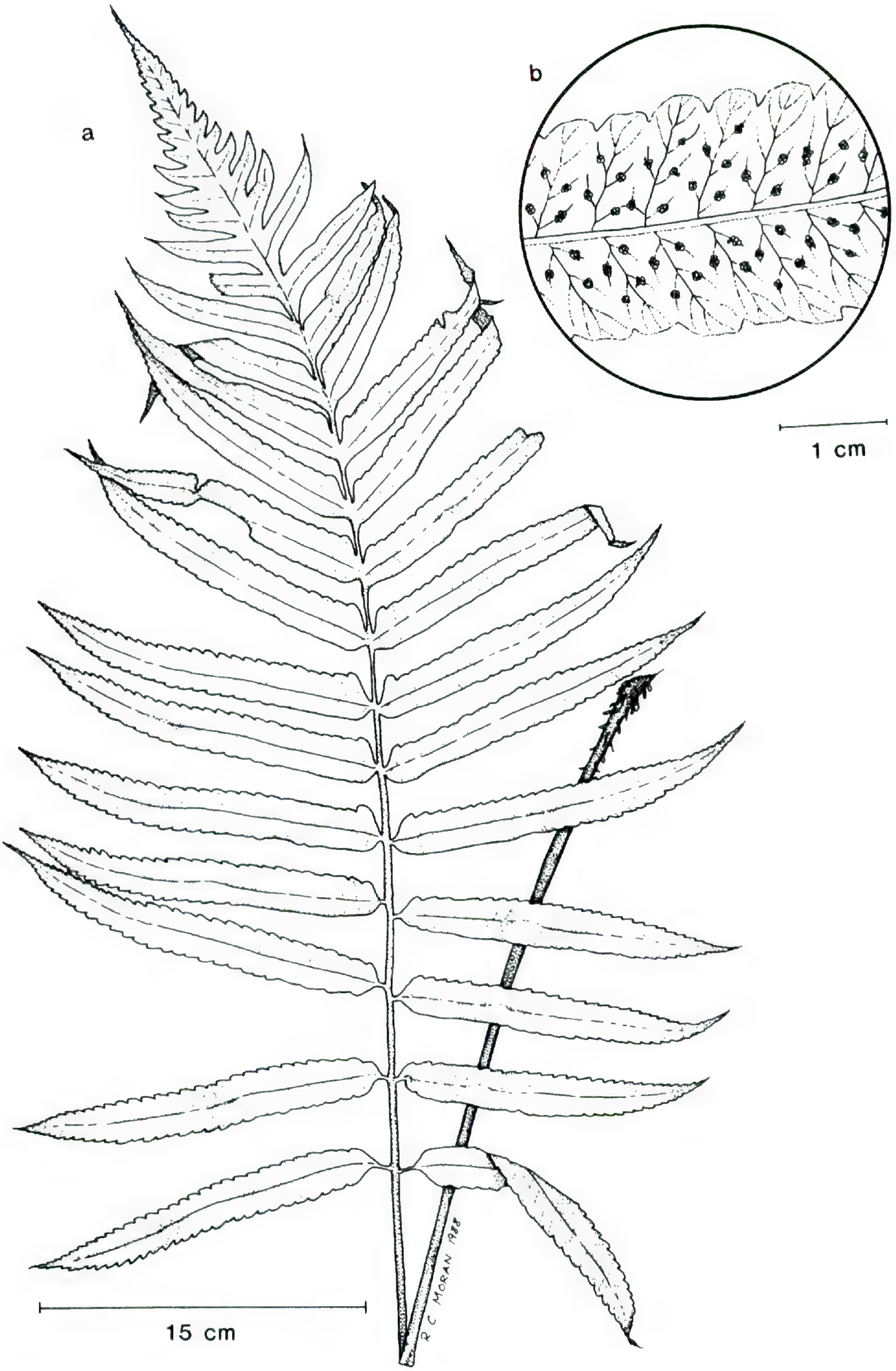


FIGURE 15. *Stigmatopteris heterocarpa* (*Oliviera & Cordeiro 909*, MO).—a. Leaf.—b. Venation and sori.

del Gato, *Ravins 961* (UC). SANTIAGO DE CUBA: Sierra Maestra, Loma de San Juán, near Loma del Gato, 1,000 m, *Clement 633* (NY), 900–950 m, *674* (P, US), 1,000 m, *945* (US), 1,000 m, *949* (P), *Fre. León et al. 10311* (US), *10409* (NY, US), *10486* (NY, US); Maestra Ridge, 1,300 m, *Fre. León 11133* (NY, US).

Stigmatopteris hemiptera is endemic to the Sierra Maestra mountains of eastern Cuba where it occurs in wet forests from 900 to 1,500 m. A diagnostic characteristic of this species is that the basal basiscopic lobes of the distal pinnae are adnate to the rachis, not the costae (Fig. 14a). Apparently, the buds are only on sterile leaves, unlike the closely related *S. gemmipara*, which has buds on the sterile and fertile leaves. This observation, however, should be confirmed by field studies, as there are few specimens of each species.

8. Stigmatopteris heterocarpa (Fée) Rosenstock, Repert. Spec. Nov. Regni Veg. 21: 347. 1925. *Phegopteris heterocarpa* Fée, Crypt. Vasc. Brésil 1: 100, t. 30, fig. 2. 1869. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Glaziou 2401* (holotype, P; isotypes, K, P). Figure 15.

Polypodium carrii Baker in C. Martius, Fl. Bras. 1(2): 597. 1870. *Dryopteris carrii* (Baker) C. Chr., Index Filic. 257. 1905. *Stigmatopteris carrii* (Baker) C. Chr., Bot. Tidsskr. 29: 298. 1909. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Carr s.n.* (holotype, K).

Stigmatopteris heterocarpa var. *basilaris* Rosenstock, Repert. Spec. Nov. Regni Veg. 21: 347. 1925. TYPE: Brazil. São Paulo: município Iguape, Morro das Pedras, *Brade 8231* (holotype, S not seen; isotype, US).

Rhizosome short-creeping; leaves to 1.5 m, petiole ca. equaling the lamina, stramineous to brown, scaly at the base, the scales 5–12 × 1–2 mm, brown, thin, lanceolate; lamina 1-pinnate-pinnatifid, lanceolate, lacking bulblets, only a few distalmost pinnae with short-decurrent bases; pinnae 14–23 × 1.7–3.2 cm, 12–17 pairs, nearly entire, crenate, or cut ¼ to the costa, the base sessile or nearly so, the basal pinnae short-stalked; lobes entire; rachis and costae stramineous, sparsely scaly, the scales ovate, lanceolate, or oblong; veins free, not forked, 3–5 per lobe; sori medial to inframedial; indusial scale absent.

Additional specimens examined. BRAZIL. MINAS GERAIS: Serra da Babilonia, 6 Apr. 1868, *Glaziou 2400* (P). PARANÁ: Desvio Ypiranga, *Dusén 8187* (BM, US); Porto de Cima, *Dusén 10244* (GH, NY, US), *14115* (B, GH), 200 m, *14680* (F, G, GH, NY, US); município Morretes, Estr. da Graciosa, Grota Funda, *Hatschbach 10748* (B, LIL), 500 m, *24376* (UC); município Tijucas do Sul, Rod. Br 468, Rio Itararé, 900 m, *Hatschbach 25939* (NY, UC, US); município Morretes, Jurapê, *Hatschbach 41955* (UC, Z); município Morretes, Estação Marumbi, *Kummrow & Hatschbach 2536* (MU, UC, US); município Morretes, Véu de Noiva, *Oliveira & Cordeiro 909* (MO, UC). RIO DE JANEIRO: Organ Mts., *Wagner 1402* (P). SANTA CATARINA: no locality, *Pabst 799* (B); Luis Alves, Itajai, *Reitz 206* (US); Antonio Carlos-Biguassú, *Reitz 259* (US); Fachinal, Biguaçú, *Reitz C919* (US); Luiz Alves, Itajaí, *Reitz 1098* (G); Azambuja, Brusque, 50 m, *Reitz 1792* (US); Mata Hoffmann, Brusque, 50 m, *Reitz 3141* (US); Horto Florestal I.N.P., Ibirama, 500 m, *Reitz & Klein 3068* (US); Blumenau, *Schenck 494* (B); município Florianópolis, Sertão da Lagoa, *Rohr 392* (GH, US), *1006* (B, UC, US); Joinville, Dec. 1904, *Schmalz s.n.* [Rosenstock, Filices austro-brasil. exsicc. no. 106] (B, GH, NY, P, UC); Morro da Cruz, *Sehnem 808* (GH); Morro do Antão, 250 m, *Sehnem 3086* (B, US); município Brusque, Azambuja, Brusque, 35–135 m, *Smith & Reitz 6127* (US); Blumenau, *Spannagel 332* (US); São Francisco, Guli, *Ule 187* (P). SÃO PAULO: município Iguape, Morro das Pedras, *8510* (UC); Peroupara, *Brade 8473* (NY, UC), *8474* (NY, UC), *8476* (NY, UC); Ilha do Cardoso, Morro da Captação, en dirección al Morro dos Tres Irmãos, 180–570 m, Rio Perequé, *Forero et al. 8793* (COL); Blumenau, Paso Mansa, *Haerchen 106* [Rosenstock, Filices austro-brasil. exsicc. no. 106] (B, P, UC).

Stigmatopteris heterocarpa is endemic to southeastern Brazil, where it grows in wet forests from 50 to 900 m. It resembles *S. rotundata*, a species of the Lesser Antilles and northern South America, but differs by its fewer pinna pairs.

It is sometimes difficult to distinguish this species from *S. tyucana*, the only difference being that *S. tyucana* has pinnae more deeply cut and generally broader than does *S. heterocarpa*. Fieldwork coupled with cytological studies may provide further evidence as to whether these two species are truly distinct.

Rosenstock's var. *basilaris* was said to differ from typical *S. heterocarpa* only by its inframedial sori. This character intergrades with medial sori and is therefore not worthy of distinction.

9. Stigmatopteris heterophlebia (Baker) R. C. Moran, Fieldiana, Bot. n.s. 27: 45. 1991. *Polypodium heterophlebium* Baker, J. Bot. 22: 363. 1884. *Dryopteris heterophlebia* (Baker) C. Chr., Index Filic. 270. 1905. TYPE: Costa Rica. Province unknown: Laguna, 305 m, *Harrison 59* (holotype, K). Figure 16. Map 3.

Rhizome short-creeping, the internodes 0.5–1 cm, the scales 1–3 mm, ovate to lanceolate, opaque, black, rigid, entire; leaves 45–100 cm; petiole ca. equaling the lamina, dull brown or tan, puberulent, scaly, the scales of two types, the first type 2–5 mm, opaque, appressed, shiny black adaxially, en-

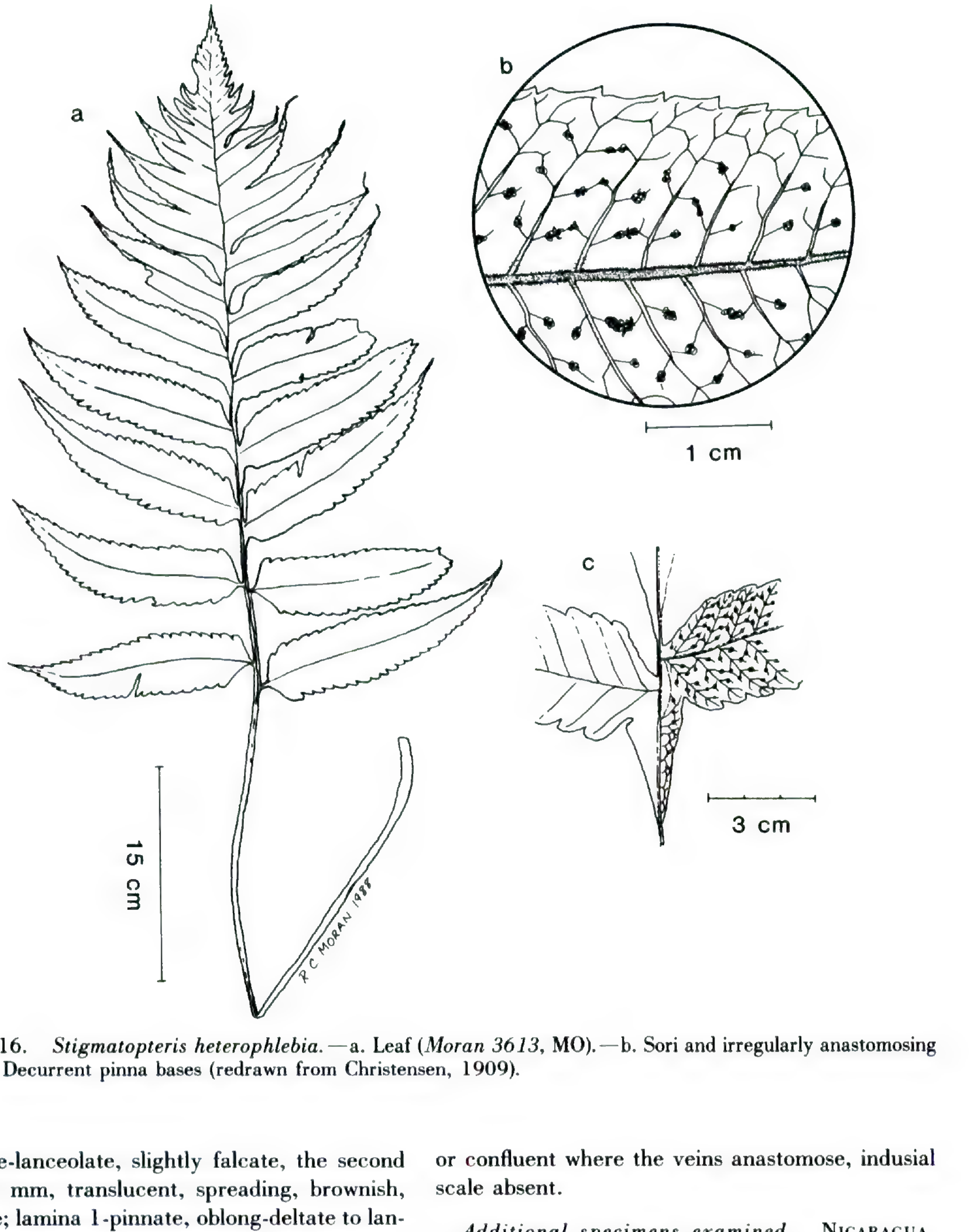
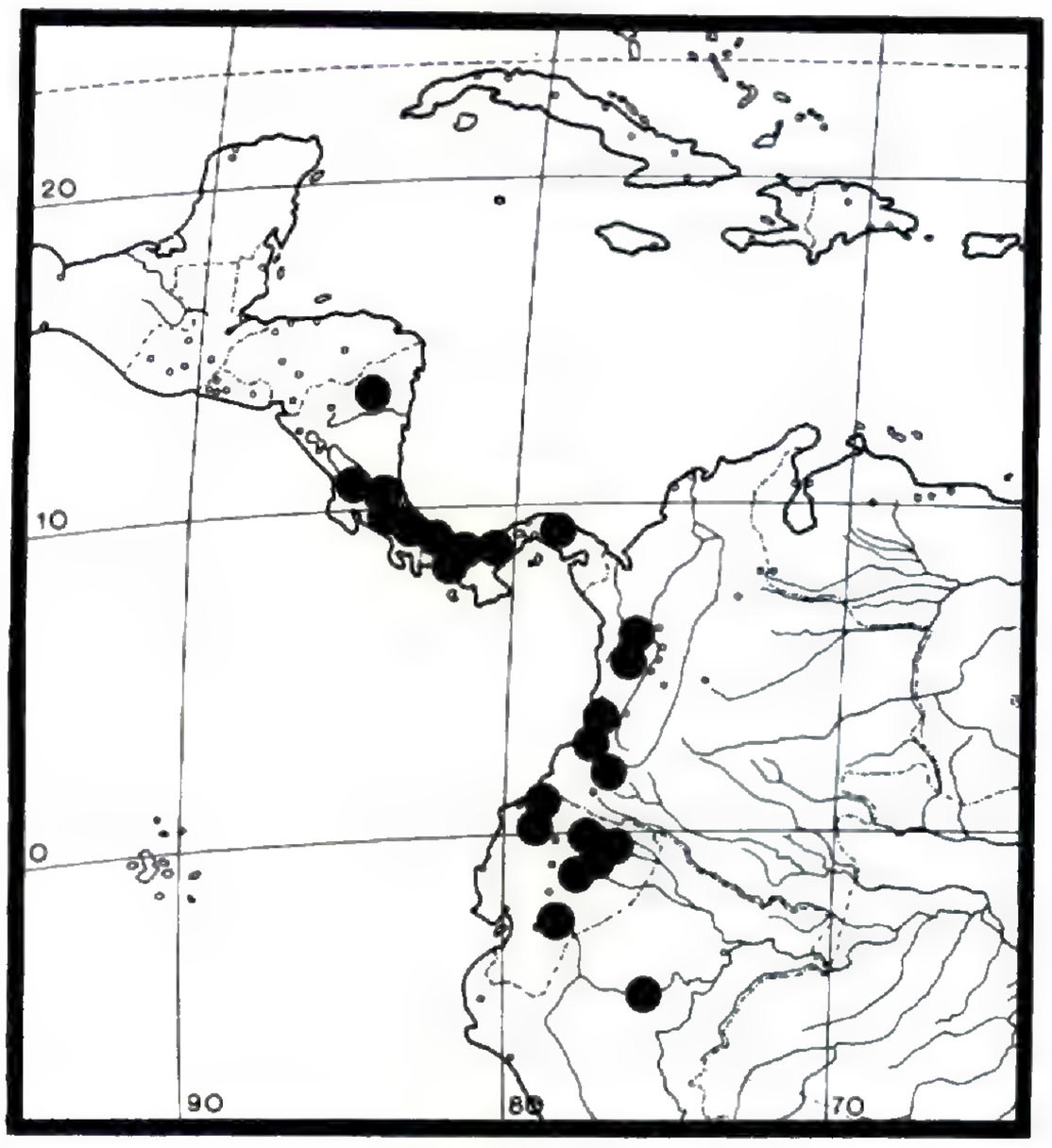


FIGURE 16. *Stigmatopteris heterophlebia.*—a. Leaf (*Moran 3613*, MO).—b. Sori and irregularly anastomosing veins.—c. Decurrent pinna bases (redrawn from Christensen, 1909).

tire, ovate-lanceolate, slightly falcate, the second type 4–9 mm, translucent, spreading, brownish, lanceolate; lamina 1-pinnate, oblong-deltate to lanceolate, buds lacking or rarely (in NW Ecuador) present; free pinna pairs 1–3(–4); basal pinnae usually somewhat reduced, widest near the middle, stalked, the stalk 2–4 mm; medial pinnae (or lobes) 10–16(–18) × 2.5–3.5(–5) cm, widest at or near the base, the margins entire to crenate, the base adnate and decurrent to or nearly to the next pinna pair; rachis and costae tan, light brown, or stramineous, puberulent and scaly, the hairs less than 0.1 mm, dense, erect, capitate-glandular (when fresh), the scales to 3 mm, lanceolate, not fibrillose; veins part free and part anastomosing; sori discrete or confluent where the veins anastomose, indusial scale absent.

Additional specimens examined. NICARAGUA. ZELAYA: Cerro Saslaya, 20 km W of Siuna, 1,100–1,400 m, *Neill 1886* (CR), *3826* (CR, MO). COSTA RICA. ALAJUELA: Reserva Forestal de San Ramón, 800–1,200 m, *Herrera Ch. et al. 162* (MO, UC), *316* (AAU, MO, NY, UC, US); canyon of Río Cariblanco and W slope and summit of ridge between Río Cariblanco and Quebrada Quicuyal, SW of Cariblanco, 840–950 m, *A. R. Smith et al. 1876* (CR, MO, UC); Univ. of San Ramón's Biological Field Station, ca. 20 km N of San Ramón, along the Río San Lorencito, 800–900 m, *Moran 4130* (CR, MO, UC); Upala, falda sur de Volcán Miravalles, *Chacón s.n.* (CR); Bajos de Jamaical Reserva de San Ramón, 700–1,000 m, *Chacón 1776* (CR); Colonia Virgen del Socorro, Sarapiquí, *Ocampo S. 1029* (CR); above San Ramón on road

to Los Angeles Norte, ca. 30 km above San Ramón, 610 m, *McAlpin 1313* (DUKE), *1326* (DUKE); Reserva de Monteverde, vertiente Pacífico, 1,520–1,580 m, *Dryer 369* (F); ca. 20 km NW of San Ramón, ca. 850 m, *A. R. Smith et al. 2253* (CR, MO, NY, UC); Univ. of San Ramón's Biological Field Station, *Moran 3188* (CR, F, GH, MO); 11 km N of San Ramón, 1,000 m, *Mickel 2955* (NY, UC, US); Univ. de Costa Rica Reserva, Fila Volcán Muerte, above the headwaters of the Río San Lorenzo, 1,000–1,300 m, *Barringer & Gómez-Laurito 2583* (F). CARTAGO: Peralta, *Lankester 893* (BM, US); SE of Turrialba, ca. 3 km NE of La Suiza, 1,200 m, *Lellinger & White 1412* (CR, F, US); SE of Orosi, ca. 2.2 km SSE of Purisil, above Finca La Concordia, 1,800 m, *Lellinger & Whtie 1476* (MICH, MO, US); Turrialba, 600 m, *Gómez 987* (CR); near Turrialba, slope of the Río Reventazón behind the Instituto Interamericano de Ciencias Agrícolas, 600 m, *Mickel s.n.* (UC); along trail leading E into mountains from road into Tapantí Reserve ca. 1 km S of jct. of Quebrada Salto and Río Grande de Orosi, 1,500–1,800 m, *A. R. Smith 2121* (CR, UC); San Juan del Norte, 1,066 m, *Scamman 7667* (GH, US); 3 km W of Turrialba, 750 m, *Mickel 2622* (NY, US); ca. 22 km E of Turrialba, high ridge above Platanillo, 1,200–1,450 m, *Mickel 3447* (NY); El Muñeco, 1,400 m, *Stork 2722* (US); El Muñeco, on the Río Navarro, 1,400–1,500 m, *Standley & Torres R. 51069* (US); Tapantí Reserve, 1,400–1,700 m, *Gómez 19288* (AAU, MO, UC). GUANACASTE–ALAJUELA: slopes of Miravalles, above Bijagua, ca. 1,500 m, *Gómez et al. 19173* (AAU, MO, UC). HEREDIA: Virgen del Socorro, 1,000 m, *Moran 3165* (F, MO, NY), *Wagner & Gómez 79021a* (CR); forest between Río Peje and Río Sardinalito, Atlantic slope of Volcán Barva, 700–750 m, *Grayum 6651* (MO, UC); between Quebrada Tigre and E fork of Río Sardinal, ca. 9 km SW of Las Horquetas, ca. 600 m, *Grayum et al. 5043* (CR, MO, UC); Tirimbina, 213 m, *Proctor 32327* (F, MO); Cerro Gallito, 1,800 m, *Valerio 295* (US); S slopes of Cerro Zurquí, 5 km N of San Luis Norte, 1,800 m, *Stolze 1634* (CR, F, UC, US). LIMÓN: vic. of Guápiles, 300–500 m, *Standley 37169* (GH, US); along Río Costa Rica, SW of Guápiles, 300 m, *Grayum et al. 3288* (MO, UC). PUNTARENAS: Monte Verde Reserve, Sendero Brillante, 1,500 m, *Hammel & Zuchowski 13880* (MO). SAN JOSÉ: La Palma, 1,400 m, *Brade 481* (GH, NY, UC); Estación Carrillo de 700 a 450 m de la Fila al Cañón del Río Sucio, *Chacón & Herrera 1624* (CR, MO, UC); Parque Nacional Braulio Carrillo, Estación La Montura, 1,050 m, *Gómez et al. 20858* (CR, MO, UC, US); Zurquí, 1,900 m, *Gómez 3522* (CR); along unnamed N fork of Río Zurquí, ca. 1,500–1,600 m, *A. R. Smith 1692* (NY, MO, UC). PROVINCE UNKNOWN: 1901–1905, *Wercklé s.n.* (NY, US). PANAMA. BOCAS DEL TORO: Oleoducto Road, near Continental Divide, Fortuna Dam area, 1,000 m, *Churchill et al. 4549* (MO, UC); Cerro Colorado, ca. 8.6 mi. W of Chamé, *Croat 69137* (MO, NY, UC); along road between Fortuna Dam and Chiriquí Grande, 7.3 mi. N of bridge over Fortuna Dam, 3.2 mi. N of Continental Divide, 700 m, *Croat & Grayum 60216* (MO, UC), *60217* (AAU, MO, UC); vic. of Fortuna Dam, below pass on Chiriquí Grande road, ca. 800 m, *McPherson 9730* (MO); road from Fortuna Dam to Chiriquí Grande, 3.1 mi. N of Continental Divide, 700 m, *McPherson 6774* (MO, UC). CHIRIQUÍ: El Boquete, 1,000–1,500 m, *Cornman 1180* (US), *1210* (MICH, MO, UC, US), *1284* (US); La Fortuna hydroelectric project, 1,300–1,400 m, *Hammel 2227* (AAU, CR, MO); Fortuna Dam area, N



MAP 3. Distribution of *Stigmatopteris heterophlebia*.

of reservoir, Quebrada Bonito to E of road, 1,100 m, *Churchill 5255* (MO); vic. of Cerro Colorado, above San Felix, 1,450 m, *McPherson 12677* (MO); Dtto. Boquete, Fortuna dam site, along trail following Continental Divide, 1,100 m, *van der Werff & van Hardeveld 6762* (MO, NY, UC); along road between Fortuna Lake and Chiriquí Grande, 4.5–5 km N of dam over Fortuna Lake, 1,100–1,135 m, *Croat & Grayum 60043* (MO); along road between Gualaca and Fortuna Dam site 7.9 mi. beyond (NW of) Los Planes de Hornito, 1,300 m, *Croat 49916* (MO); vic. of Fortuna Dam in valley of Río Chiriquí, along aqueduct trail for water supply to IRHE facilities, 1,100–1,200 m, *Croat 66559* (AAU, MO, NY, UC); valley of the Río Piarnasta, ca. 5 mi. E of El Boquete, 1,525–1,600 m, *Killip 5387* (F, UC, US). COCLÉ: valle de Antón, 1,000 m, *Alston 8745* (BM, MO). PANAMÁ: trail from end of road past Los Altos de Pacora region of Cerro Jefe, on to Cerro Brewster, 600–800 m, *Hammel & de Nevers 13578* (MO, UC). VERAGUAS: 3 mi. from Escuela Agrícola Alto Piedra on road to Río Calovébora, 731 m, *Antonio 2050* (CR, MO); valley of Río Dos Bocas on road between Alto Piedra (above Santa Fé) and Calovébora, 350–400 m, *Croat 27477* (MO, NY); on Caribbean slope above Río Primero Brazo, 5 mi. NW of Santa Fé, 700–1,200 m, *Croat & Liesner 1010* (MO). COLOMBIA. CAUCA: Coteje, Río Timbiqui, *Lehmann 8951* (F, GH, K, US); Cordillera Oriental, comisaria of Putumayo, Oreto (Indian pueblo) on Río Oretopungo, tributary of Río Putumayo, 450 m, *Ewan 16775* (BM, UC, US). CHOCÓ: Municipio de San José del Palmar, hoya del Río Torito, afluente del Río Hábita, 850–950 m, *Forero et al. 7407* (MO); Carretera Ansermanuevo–San José del Palmar, entre el Alto del Galapago y San José del Palmar, 1,900 m, *Forero et al. 2309* (COL, MO). EL VALLE: Costa del Pacífico, Río Cajambre, San Isidro, 5–100 m, *Cuatrecasas 17336* (US). ECUADOR. ESMERALDAS: banks of Río Palaví, 0.5 km below Awá encampment, 100 m, *Hoover et al. 4304* (MO, UC), *4325* (MO, UC). MORONA–SANTIAGO: along new road Méndez–Morona, 650 m, *van der Werff & Gudiño 11125* (MO, UC). NAPO: Añangu, Parque

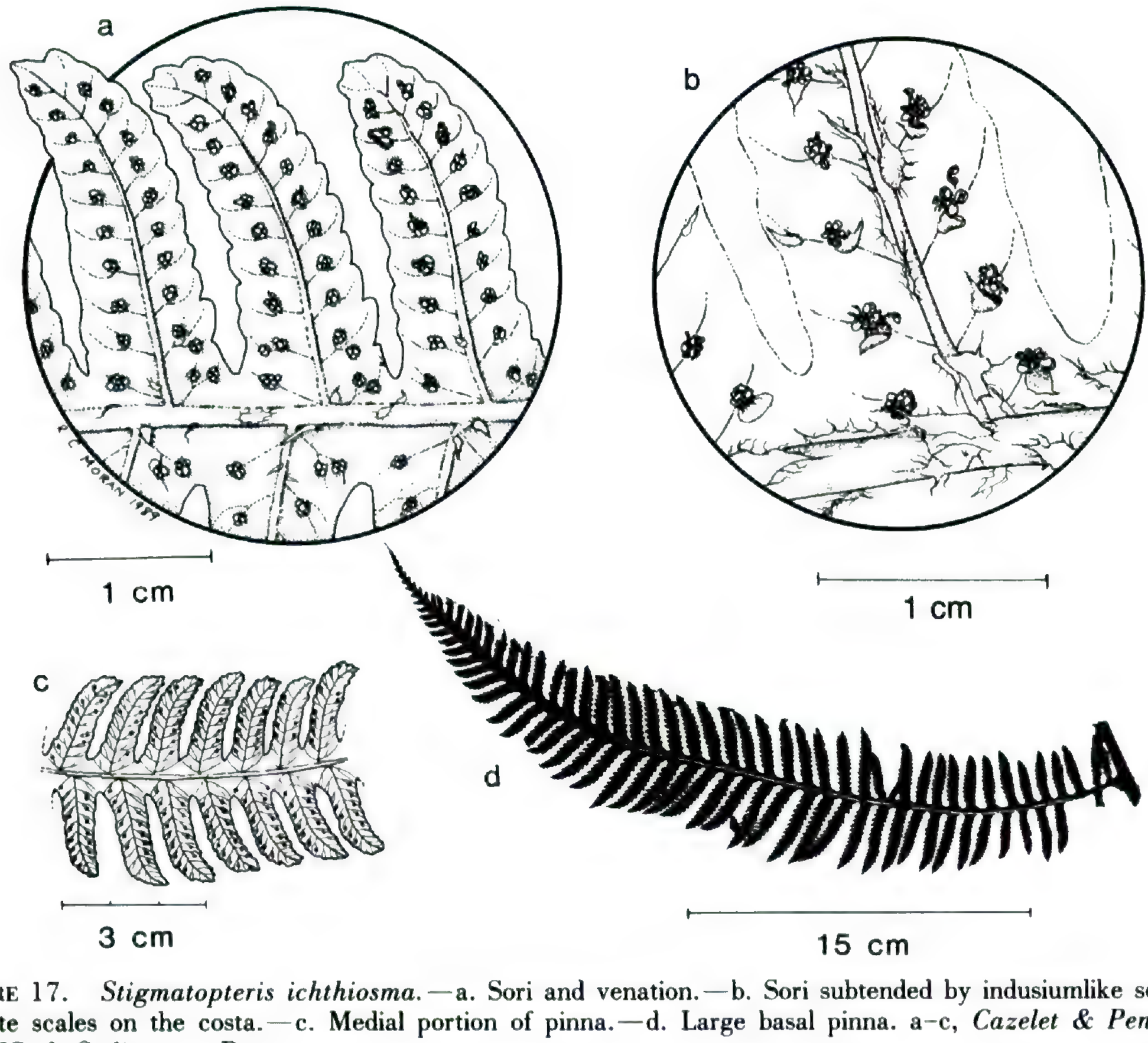


FIGURE 17. *Stigmatopteris ichthiosma.*—a. Sori and venation.—b. Sori subtended by indusiumlike scale and lanceolate scales on the costa.—c. Medial portion of pinna.—d. Large basal pinna. a–c, *Cazelet & Pennington 5276*, UC. d, *Sodiro s.n.*, P.

Nacional Yasuní, 260–350 m, *Øllgaard et al. 39229* (AAU); 12 km SW de Coca, por el camino se llama Los Zorros, 240, *Moran 3613* (MO); Estación Experimental de INIAP, San Carlos 6 km al SE de Los Sachas, 250 m, *Baker 5934* (NY); at Río Payamino 60 km along Río Payamino W of Coca, 350 m, *Holm-Nielsen & Jeppesen 811* (AAU, GH). PICHINCHA: NE of Vicente Maldonado, Reserva de ENDESA, 600 m, *Laegaard 51611* (AAU, MO). PERU. LORETO: Santa Rosa, lower Río Huallaga below Yurimaguas, ca. 135 m, *Killip & Smith 28984* (NY, US).

Stigmatopteris heterophlebia occurs from Nicaragua to Peru (Map 3) in wet forests from 100 to 1,900 m. It resembles *S. bulbifera* in its glandular hairs that densely cover the axes but differs from that species by its few free pinna pairs. A further difference is that *S. heterophlebia* usually lacks buds, whereas *S. bulbifera* has them on the adaxial surface of the rachis—costae junctures. This characteristic is not completely constant because two specimens of *S. heterophlebia* from the department of Esmeraldas, Ecuador, have buds.

This species is also variable in the scaliness of the axes. Several specimens from Costa Rica and Panama (*Hammel & de Nevers 13578, Lellinger & White 1692, Croat & Liesner 1010*) are extremely scaly but are typical in all other characteristics, and no other feature seems to correlate with the scaliness.

Stigmatopteris heterophlebia has been previously called *S. alloëoptera* (Kunze) C. Chr., a name that cannot be used because it is of uncertain application (see section on names of uncertain application).

10. Stigmatopteris ichthiosma (Sodiro) C. Chr., Bot. Tidsskr. 29: 302. 1909. *Polypodium ichthiosmum* Sodiro, Recens. Crypt. Vasc. Quit. 59. 1883, as *ichtiosmum* in Sodiro, Crypt. Vasc. Quit. 294. 1893. *Dryopteris ichthiosma* (Sodiro) C. Chr., Index Filic. 271. 1905. TYPE: Ecuador, "Atcao, 1,500 m, S. Florencia, etc." *Sodiro s.n.* (holotype, Q; isotypes, BM, K, P). Figure 17.

Polypodium dentatum Baker, Ann. Bot. (London) 5: 456. 1891, nom. illeg., not Forssk. 1775. *Dryopteris longipetiolata* C. Chr., Index Filic. 275. 1905, nom. nov. for *P. dentatum* Baker. TYPE: Ecuador. "Andes of Ecuador," *Sodiro s.n.* (holotype, K).

Rhizome short-creeping; leaves to 2 m long;

petiole ½ to equaling the length of the lamina, brown, scaly, the scales 4–6 × 2–2.5 mm, ovate, symmetrical, occasionally with darkly sclerified abaxial surfaces, the base cordate (appearing false-peltate), fibrillose scales absent; lamina 1-pinnate-pinnatifid, lanceolate, lacking bulbils; pinnae 20–40 × 2.5–6 cm, 15–20 pairs, cut ca. ⅔ to the costa, sessile or the basal ones short-stalked, the stalk 2–7 mm; segments 4–10 mm wide, serrate at the apex, the sides entire, serrate or rarely lobed, basal basiscopic segment not reduced; rachis and costae stramineous or brown, scaly, the scales non-bullate, ovate, lanceolate, or filiform; veins free, 7–14 per segment, unbranched or 1-forked with a short acroscopic branch which in fertile segments bears the sorus; sori with an indusiumlike scale.

Additional specimens examined. ECUADOR. CHIMBORAZO: red bark woods of Chimborazo, Río Chasnan, *Spruce 5714* (BM). PICHINCHA: "Andes of Quito," *Sodiro s.n.* (AAU, P, Q); Toachi, Sep. 1874, *Sodiro 48/1* (K); 20 km W of Santo Domingo de los Colorados, 300 m, *Cazelet & Pennington 5276* (NY, UC, US); road Chillogallo–Santo Domingo below Chiriboga, 16 km from the new road, 1,600 m, *Holm-Nielsen et al. 24819* (AAU); Maquipucuna Biological Field Station, ca. 5 km S of Nanegalito and ca. 25 km N of Quito, 1,400–1,700 m, *Moran 5250* (MO, QCNE); 2.5 km E of Cornejo Astorga, 1,200 m, *Moran 3545* (MO, Q, QCA). PROVINCE UNKNOWN: near Río Blanco, 1,800 m, *Mille s.n.* (P); near Angamarca, 12/905, *Sodiro s.n.* (P); no location, *Stübel 797* (B).

Stigmatopteris ichthiosma occurs in the western Andes of Ecuador in wet forests from 300 to 1,800 m. It resembles *S. pellucidopunctata* in leaf shape and cutting, but differs by its ovate to lanceolate (rather than filiform) scales on the abaxial surface of the axes, ovate (rather than lanceolate-falcate) petiole scales, and the presence of an indusiumlike scale that subtends the sorus (rather than none). Furthermore, *S. ichthiosma* occurs only in the western Andes, whereas *S. pellucidopunctata* occurs only on the eastern side of the Andes.

The specific epithet is usually spelled *ichtiosma*; however, Sodiro's (1883) original spelling is *ichthiosma*. He later altered it to *ichtiosma* but did not give a reason (Sodiro, 1893). According to Sodiro (1883), the dried plant smells like fish, thus the specific epithet from the Greek *icthys*, fish, and *osme*, odor. I prefer to maintain the original spelling because its derivation is clear and because Article 73.1 of the *Code* (Greuter et al., 1988) states that the author's original spelling should be maintained. I cannot, however, detect a fishlike odor from the dried plants.

Christensen (1909, 1913) listed this species from Cuba and Jamaica; however, the specimens he cited represent two closely related species: *S. hemiptera* (Maxon) C. Chr. (endemic to Cuba) and *S. jamaicensis* (Desv.) Proctor (endemic to Jamaica).

The other Ecuadorian specimens collected by Sodiro (see specimens examined) might also be types, because he says "etc." for the type localities, meaning other sites on the western slopes of the Andes.

11. Stigmatopteris jamaicensis (Desv.) Proctor, Brit. Fern Gaz. 9: 221. 1965. *Cystopteris jamaicensis* Desv., Mém. Soc. Linn. Paris 6: 263. 1827. TYPE: "Habitat in Antillis" [undoubtedly Jamaica], *Tussac s.n.* (holotype, P; photos, BM, GH, UC, US ex P). Figure 18.

Dryopteris nothochlaena Maxon, Contr. U.S. Natl. Herb. 24: 58. 1922. *Stigmatopteris nothochlaena* (Maxon) C. Chr., Index Filic. Suppl. 3: 174. 1934. TYPE: Jamaica. St. Thomas: near Cuna Cuna Pass, 610–823 m, *Maxon 1738* (holotype, US).

Rhizome erect, compact; leaves to 2 m long; petioles ca. ½ the length of the lamina, stramineous to brown, glabrate to densely scaly (especially toward the base), the scales 1–1.5 cm, spreading, ovate-lanceolate; lamina 1-pinnate-pinnatisect, or fully 2-pinnate at the base, oblong to lanceolate, lacking buds; pinnae 15–23 × 2–4(–5) cm, 22–26 pairs, widest at or below the middle, cut ⅞ to nearly to the costa, the base sessile or nearly so; segments 3–7 mm wide, serrate, the apex rounded; rachis and costae stramineous, scaly, the scales ovate to lanceolate, those of the costules bullate; veins free, 8–11 per segment, mostly simple, not forked, scaly, the scales ovate, bullate; sori covered by an indusiumlike scale similar to those on the veins.

Additional specimens examined. JAMAICA. CLARENDON: Second Breakfast Spring, below Tweedside, 610 m, *Underwood 1613* (NY, US); Tweedside, *Harris 7419* (BM, NY), *Underwood 2036* (NY). PORTLAND: Mabess River, E bank, Blue Mts., *Papenfuss s.n.* (UC); Mabess River, ca. 1,158 m, *Watt 82* (P), *102* (P), *Skutch 145* (US); Mabess River, below Vinegar Hill, 915 m, *Underwood 1315* (NY); trail from Morces Gap to Vinegar Hill, 1,175–1,500 m, *Maxon & Killip 716* (F, GH, NY, US); Seamen's Valley, 150–250 m, *Maxon & Killip 7* (F, GH, NY, US); Dollwood, 915 m, *Harris 7277* (NY), *Jenman s.n.* (NY); Hardwar Gap, 1,219 m, *Crosby et al. 521* (DUKE, GH, MICH); spur of John Crow Mts. opposite Mill Bank, 450–625 m, *Maxon 9307* (NY, US). ST. ANNE: Blue Mts., Trafalgar, *Perkins 1161* (G, GH). ST. THOMAS: Mansfield and adjoining properties, near Bath, 300–500 m, *Maxon 2388* (NY, US); Mansfield near Bath, 1861, *Gilbert s.n.* (BM, GH); Corn Puss Gap and vicinity, trail W over Blue Mts., 610 m, *Wilson & Murray 563* (GH, MICH); Cuna Cuna trail, above Mattis River,

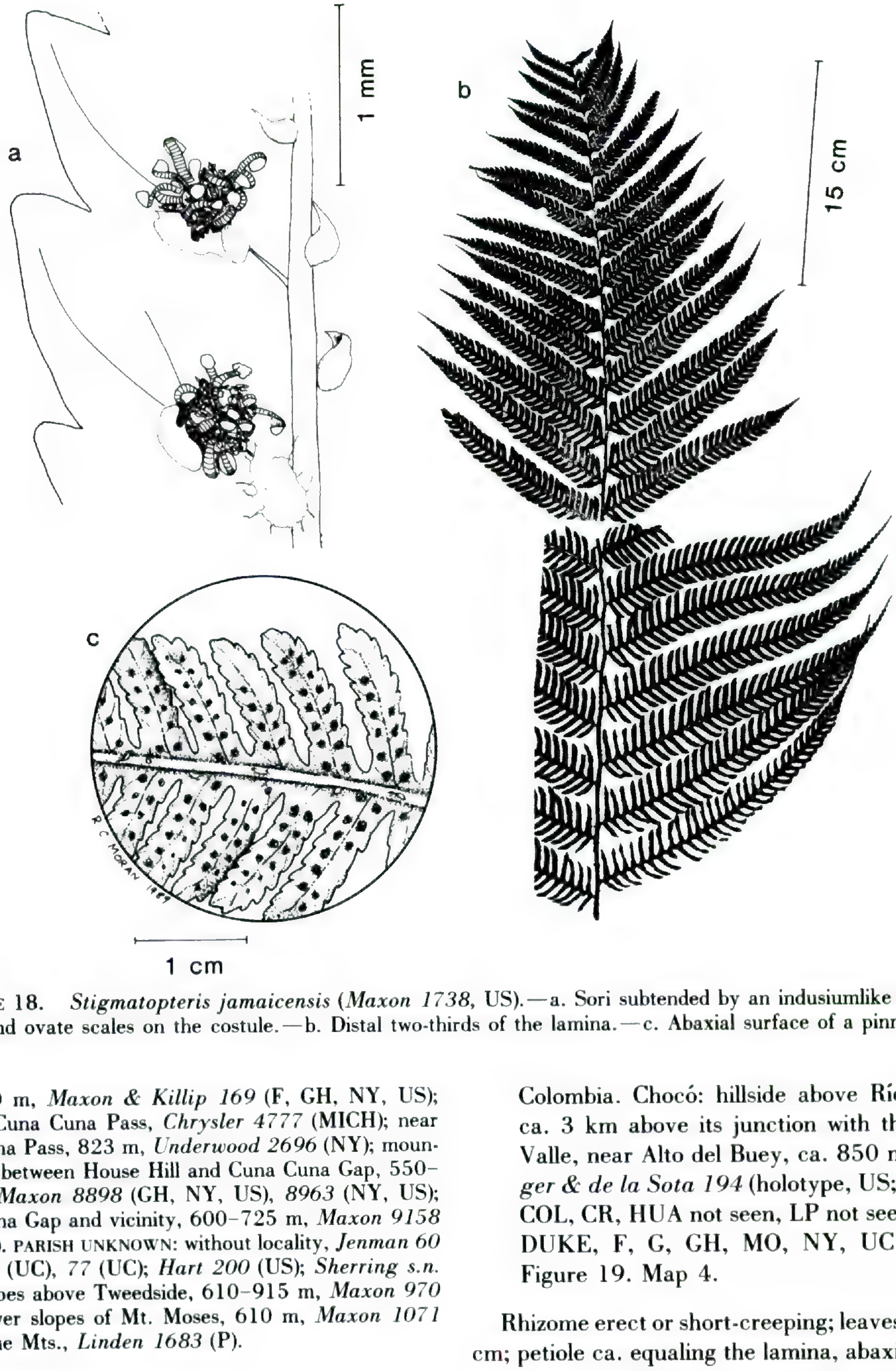


FIGURE 18. *Stigmatopteris jamaicensis* (*Maxon 1738*, US).—a. Sori subtended by an indusiumlike scale, and bullate and ovate scales on the costule.—b. Distal two-thirds of the lamina.—c. Abaxial surface of a pinna.

300–500 m, *Maxon & Killip 169* (F, GH, NY, US); Bath to Cuna Cuna Pass, *Chrysler 4777* (MICH); near Cuna Cuna Pass, 823 m, *Underwood 2696* (NY); mountain trail between House Hill and Cuna Cuna Gap, 550–725 m, *Maxon 8898* (GH, NY, US), *8963* (NY, US); Cuna Cuna Gap and vicinity, 600–725 m, *Maxon 9158* (GH, US). PARISH UNKNOWN: without locality, *Jenman 60* (UC), *62* (UC), *77* (UC); *Hart 200* (US); *Sherring s.n.* (US); slopes above Tweedside, 610–915 m, *Maxon 970* (US); lower slopes of Mt. Moses, 610 m, *Maxon 1071* (US); Blue Mts., *Linden 1683* (P).

Stigmatopteris jamaicensis is endemic to Jamaica where it grows in wet forests, 150–1,200(–1,500) m. It can be distinguished from all other species of *Stigmatopteris* by the bullate scales on the costules. Walker (1966) counted the chromosomes of this species and found that $n = 41$. This is the only count known for the genus.

12. Stigmatopteris killipiana Lellinger, Proc. Biol. Soc. Wash. 89: 730, fig. 8. 1977. TYPE: Colombia. Chocó: hillside above Río Mutata ca. 3 km above its junction with the Río El Valle, near Alto del Buey, ca. 850 m, *Lellinger & de la Sota 194* (holotype, US; isotypes, COL, CR, HUA not seen, LP not seen; photos DUKE, F, G, GH, MO, NY, UC ex US). Figure 19. Map 4.

Rhizome erect or short-creeping; leaves 70–150 cm; petiole ca. equaling the lamina, abaxially atro-purpureous and lustrous, adaxially stramineous or tan, scaly and with a scurf, the scales of two types, the first type 2–5 mm, opaque, appressed, shiny black abaxially, entire, ovate-lanceolate, slightly falcate, the second type 4–9 mm, translucent, spreading, brownish, lanceolate, the scurf appressed, arachnoid, cauducous, light brown or tan; lamina 1-pinnate, oblong-deltate to lanceolate, buds lacking, free pinna pairs 5–13; medial pinnae 14–18(–26) × 3–4.5 cm, widest at or just above the

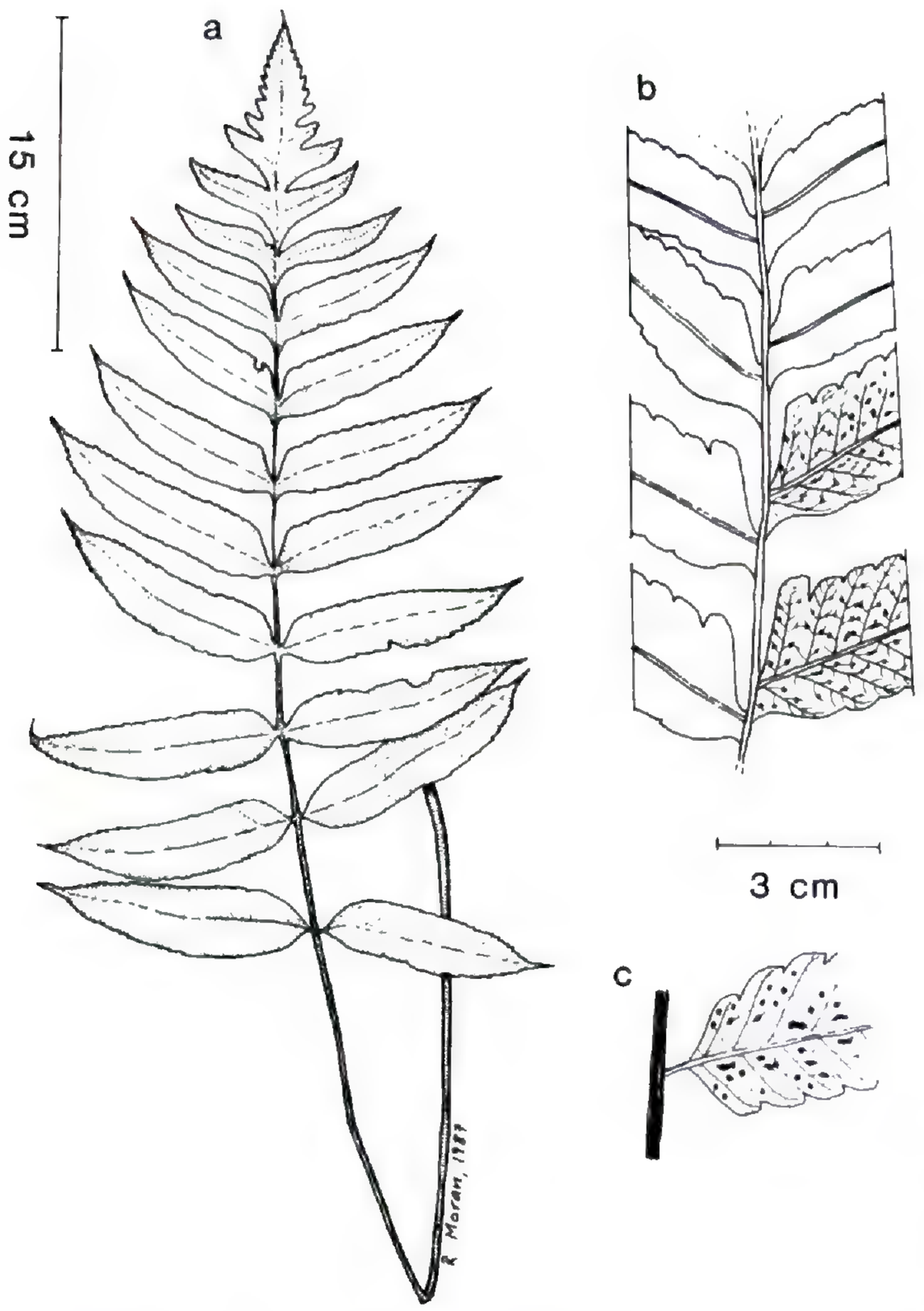
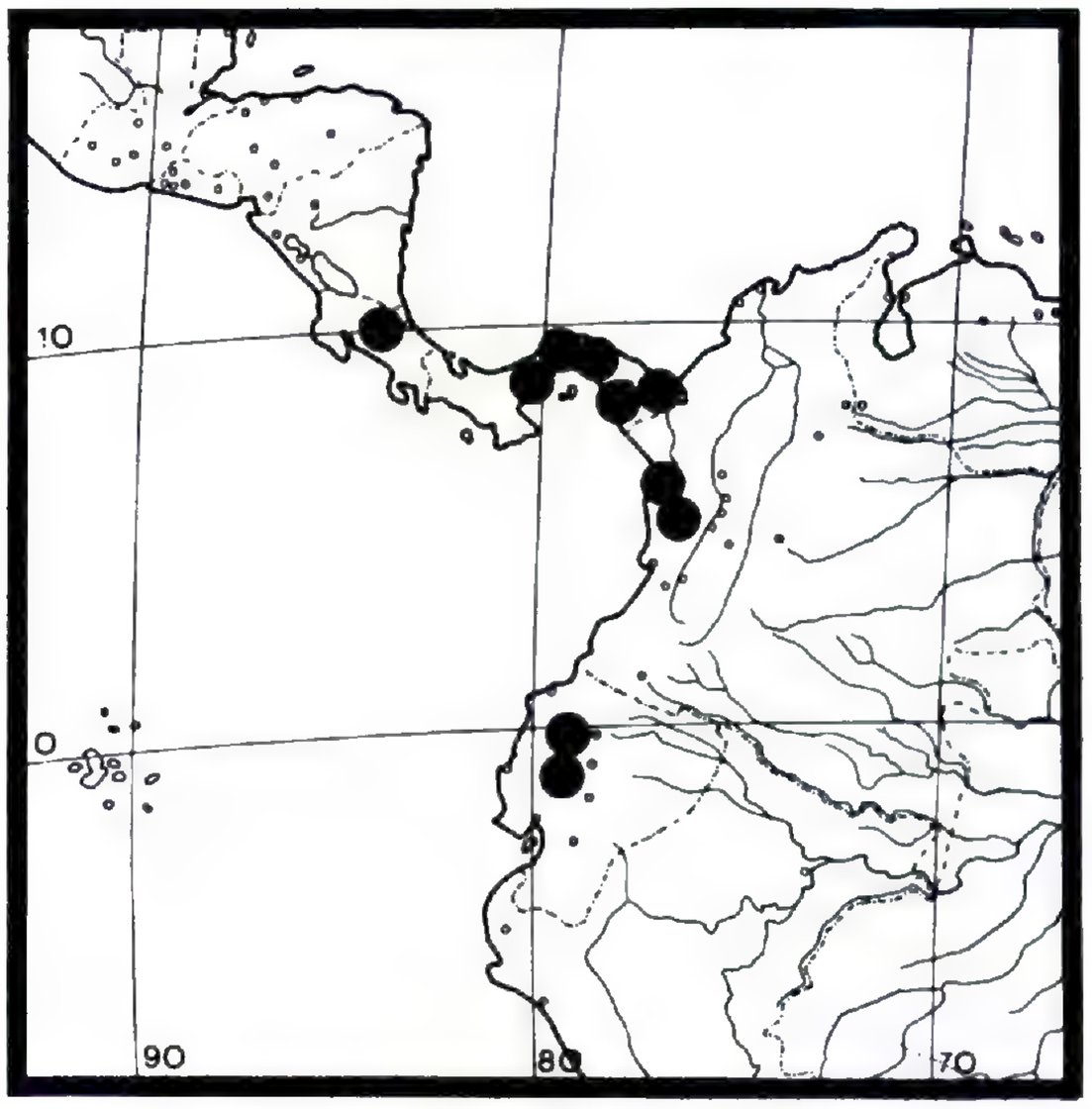


FIGURE 19. *Stigmatopteris killipiana*.—a. Leaf (*Moran 3611*, MO).—b. Distal part of the lamina showing the transition from decurrent to nondecurrent pinna bases (*Grayum et al. 5495*, MO).—c. Basal portion of a basal pinna (*Grayum et al. 5495*, MO).



MAP 4. Distribution of *Stigmatopteris killipiana*.

base, the margins entire to crenate, the base sessile, the upper pinnae with a short decurrent base; basal pinnae ca. equaling the above pinnae, widest at or just below the middle, stalked, the stalk 2–3 mm; rachis atropurpureous at the base, the costae stramineous, both axes lacking hairs, scaly, the scales lanceolate to linear, not fibrillose, scattered; veins partly free and partly anastomosing irregularly; sori discrete or confluent with adjacent one where the veins anastomose, an indusial scale lacking.

Additional specimens examined. COSTA RICA. SAN JOSÉ: hills at SW part of Montañas Jamaica, ca. 2.5 km NE of Bijagual de Turrubares, Carara Reserve, 460–520 m, *Grayum et al. 5495* (MO). PANAMA. CANAL ZONE: Pipeline road from Gamboa, *Armond 557* (DUKE); NW of Gamboa along "Pipeline Road," *McAlpin 1396* (DUKE); near Frijoles, *Killip 2919* (US); between Frijoles and Monte Lirio, 30 m, *Killip 12147* (GH, US). COCLÉ: El Valle de Anton, 800 m, *Alston 8803* (BM, MO), 700 m, *Alston 8848* (AAU, BM, CR, F, UC, US); Parque Nacional Soberanía, camino del Oleoducto, Río Pilón, *Vásquez 209* (UC), *245* (UC). DARIÉN: Cerro Sapo, ca. 5 km S of Garachiné, along ridge at north approach to cerro, in mixed forest just above *Phytelephas* slope, 600–800 m, *Hammel et al. 14827* (MO); middle slopes on the W side of Cerro Pirre, 550–760 m, *Croat 68882* (MO). PANAMÁ: along road to Alto de Pacora, 2 km N of turnoff to Cerro Jefe radio tower, *Hammel 4858* (CR, MO). COLOMBIA. CHOCÓ: Municipio de Nóvita, vereda Curundó, margen izquierda del Río Ingará, 720 m, *Franco et al. 1148* (COL). ECUADOR. LOS RÍOS: Río Palenque Biological Station, km 56 N of Quevedo, 150–220 m, *Moran 3611* (MO, QCA), *Evoy 44* (NY), *Grayum & Zamora 9375* (MO, UC). PICHINCHA: Hotel Tinalandia, ca. 25 km E of Santo Domingo de Los Colorados, N side of Río Toachi, 1,000 m, *Moran 3562* (MO, QCA).

Stigmatopteris killipiana grows in and along streambeds from Costa Rica to Ecuador (Map 4), from 30 to 1,000 m. It differs from the similar species *S. pterorhachis* and *S. heterophlebia* by its atropurpureous rachis with abundant scurf and by the greater number of free pinna pairs (5–13) beneath the pinnatifid apex. It further differs from *S. heterophlebia* by its nonpuberulent axes.

13. Stigmatopteris lechleri (Mett.) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 8, 6: 28. 1920. *Phegopteris lechleri* Mett., Fil. Lechler. 2: 25. 1859. TYPE: Peru. Puno: San Gabán, *Lechler 2497* (holotype, B; fragments, BM). Figure 20. Map 5.

Polypodium cyclocolpon Bommer & Christ, Bull. Herb. Boissier sér. 2, 4: 659. 1896 [Bull. Soc. Roy. Bot. Belgique 35: 216. 1896]. *Dryopteris cyclocolpa* (Bommer & Christ) C. Chr., Index Filic. 260. 1905. *Stigmatopteris cyclocolpa* (Bommer & Christ) C. Chr., Amer. Fern J. 4: 82. 1914. TYPE: Costa Rica. Limón: Forêts de Tsâki, Talamanca, 200 m, Apr. 1885, *Tonduz 9480* (holotype, BR not seen; isotypes, US, fragment B, photo BM ex BR).

Stigmatopteris ecuadorensis C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 8, 6:

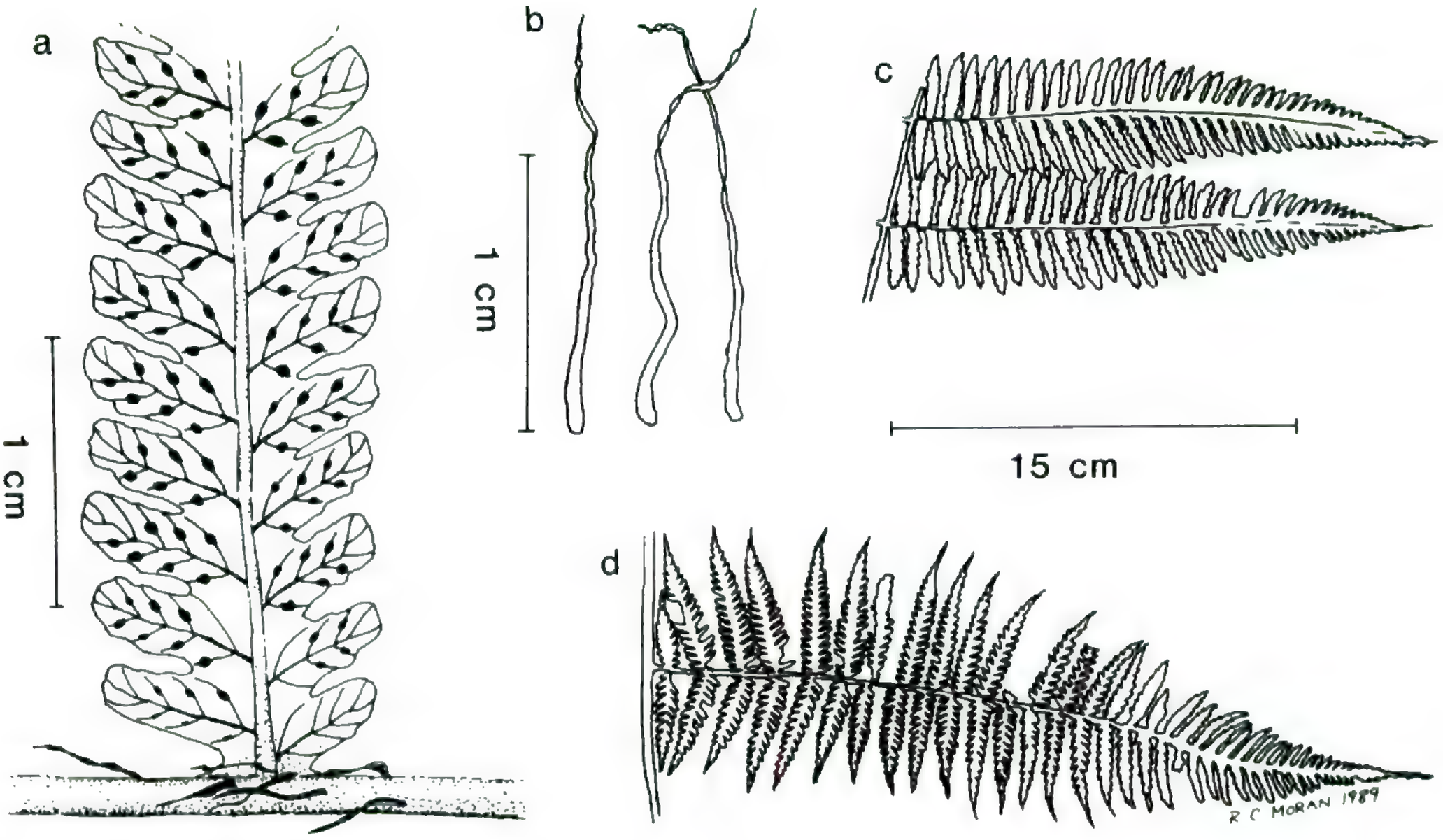


FIGURE 20. *Stigmatopteris lechleri* (*Moran 3582*, MO). —a. Basal part of pinnule. —b. Petiole scales. —c. Medial pinnae. —d. Basal pinna.

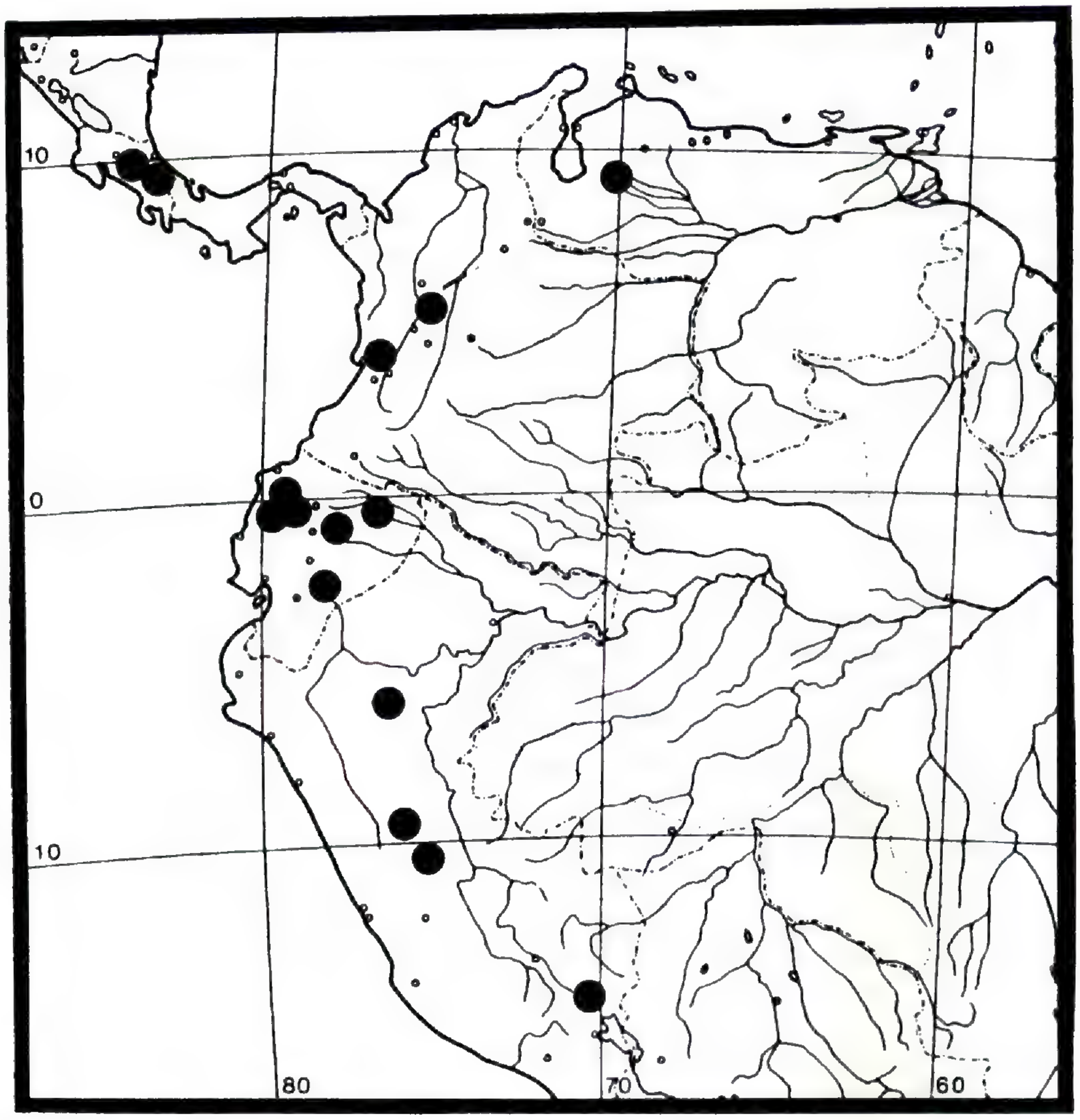
29. 1920. TYPE: Ecuador. "Andes of Quito," *Sodiro s.n.* (holotype, B; isotypes, BM, P in herb. Christ).

Polypodium punctatum Spruce in Hook., Sp. Fil. 4: 262. 1862, nom. illeg., non (L.) SW. 1802. *Polypodium prasinum* Baker, Syn. Fil. 312. 1867, nom. nov. for *P. punctatum* Hook., with the same type. *Dryopteris prasina* (Baker) C. Chr., Index Filic. 285. 1905. *Stigmatopteris prasina* (Baker) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 7, 10: 79. 1913. LECTOTYPE (designated by Christensen, 1913): Peru. San Martín: Tarapoto, Mt. Guayrapurima, Aug. 1856, *Spruce 4719* (K; isolectotypes, BM, G, P; photos F, MO ex K).

Rhizome erect-ascending; petioles ca. equaling the lamina, brown to tan, scaly, especially toward the base, the scales 8–20 × 1–2(–3) mm, lanceolate to linear, brown to blackish, the margins flat or enrolled, entire; lamina 2-pinnate-pinnatifid, 0.6–1.2 × 0.4–0.8 m, deltate or nearly so, bulblets absent; pinnae 25–40 × 5–15 cm, widest at the base, not overlapping the rachis; pinnules 4–10 × 1–2.3 cm, narrowly lanceolate-triangular, sessile to broadly adnate and decurrent, lobed to pinnatisect; lobes oblong to rectangular, entire to serrate apically; rachis and costae stramineous or brown, scaly, the scales linear or narrowly triangular, tortuous, fibrillose; veins unbranched or rarely (in the larger segments) branched, nearly reaching the margin; sori lacking an indusial scale.

Additional specimens examined. COSTA RICA. LIMÓN: Cantón de Talamanca, Amubri, margen izquierda del Río Urén, Loma Sheub, 150 m, *Herrera Ch. 2980* (CR, MO). Zona Protectora Barbilla, W side of plateau separating headwaters of N fork of Río Dantas from headwaters of Quebrada Barreal, Río Barbilla drainage, 600–660 m, *Grayum et al. 7922* (MO, UC, US). VENEZUELA. PORTUGUESA: Dtto. Sucre, Villa Rosa, 15 km SE de Biscucuy, bosques nublados a lo largo de la quebrada El Potrero, 1,400–1,600 m, *Aymard et al. 3747* (NY, PORT, UC). COLOMBIA. CALDAS: Santa Cecilia, Cordillera Occidental, vertiente Occidental, 800 m, *von Sneidern 5046* (F, US). EL VALLE: Digua Valley, Río Blanco, 500 m, *Alston 7842* (BM). ECUADOR. MORONA SANTIAGO: Cordillera de Cutucú, western slopes, along trail from Logroño to Yaupi, 1,600 m, *Madison et al. 3472* (GH, QCA). NAPO: 15 km N of Tena along road to Baeza, 1,100 m, *Moran 3582* (MO, QCA, QCNE); Cantón Archidona, faldas S del Volcán Sumaco, carretera Hollín–Loreto, km 31, comuna challa Yacu, 1,200 m, *Palacios 4030* (MO, QCNE); *Moran 5119*, MO, QCNE; Francisco de Orellana, cerca del Cañón de los Monos en Potrero, 250 m, *Zak & Jaramillo 3635* (MO). PICHINCHA: carretera Quito–Puerto Quito, km 113, 10 km N de la carretera principal, Reserva de ENDESA, Corporación Forestal Juan Manuel Durini, 800 m, *Moya 0011* (AAU); freq. in silvis de los Colorados, Oct. 1883, *Sodiro s.n.* (SI, UC); crescit in silvis tropicis ad San Miguel, Aug. 1875, *Sodiro s.n.* (fragment, B). PERU. HUÁNUCO: 25 km NE of Tingo María, La Divisoria, 1,700 m, *Moran 3696* (MO, USM). PASCO: Provincia Oxapampa, Gran Pajonal, 2–3 km N of Chequitavo, 1,200 m, *D. N. Smith 5082* (MO).

Stigmatopteris lechleri occurs from Costa Rica to Venezuela and Peru (Map 5), from 200 to 1,700 m. It is easily identified by its 2-pinnate-pinnatifid lamina, which is the most finely divided in the genus. The petiole scales vary considerably. Specimens from most parts of the range have linear or narrowly triangular scales with inrolled margins, but specimens from Colombia have wider lanceolate scales with flat (not inrolled) margins. Since intermediate specimens exist and no other character



MAP 5. Distribution of *Stigmatopteris lechleri*.

correlates with the scale differences, the variation does not merit nomenclatural distinction.

Christensen (1920) distinguished *S. cyclocolpa* and *S. ecuadorensis* from *S. lechleri* by the degree of pinnule adnation and cutting. However, these characters are variable, even on a single leaf as one goes from the more highly divided base to the less-divided medial regions. Apparently, Christensen saw only incomplete type material, which represented the different degrees of cutting.

14. Stigmatopteris longicaudata (Liebm.) C. Chr., Bot. Tidsskr. 29: 300. 1909. *Polypodium longicaudatum* Liebm., Kongel. Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 5, 1: 209. 1849. *Dryopteris longicaudata* (Liebm.) Maxon, Contr. U.S. Natl. Herb. 13: 18. 1909. SYNTYPES: Mexico. Veracruz: "Baranca de Huitamalco," *Liebmann s.n.* [Liebm. Pl. Mex. *2694*, Flora Mex. *737, 738, 739*] (lectotype, *737*, chosen by A. R. Smith, Fl. Chiapas, Part 2, 213. 1981: C—folio herbarium not seen; isolectotype, K). Figure 21. Map 6.

Stigmatopteris palmensis Rosenstock, Repert. Spec. Nov. Regni Veg. 22: 12. 1925. TYPE: Costa Rica. San José: La Palma, *Brade & Brade 497* (holotype, S? not seen; isotypes, UC, US).

Rhizome erect or creeping, the internodes ca. 1 cm, the scales 1–2 mm, black, rigid, entire, ovate-lanceolate; leaves 0.8–1.4 m; petiole ½ to equaling the lamina, brown or less often straminеous, the scales of two types, the first type 2–5 mm, opaque, appressed, shiny black, entire, ovate-lanceolate, the second type 4–9 mm, translucent, spreading, brownish, lanceolate; lamina 1-pinnate, ovate to subdeltate, lacking bulbils; pinnae mostly 14–20 × 2–2.5 cm, linear to narrowly lanceolate, 12–20 pairs, entire, crenate, or cut less than ¼(–⅓) to the costae; pinnae confluent in the distal ½–⅓ of the lamina by the decurrent pinna bases, lower pinnae free, subsessile, or stalked, the stalk 2–5 mm; rachis and costae glabrous to densely scaly, the scales ovate to lanceolate, or (in Venezuela, Peru, and Bolivia) linear and fibrillose; veins free, or with a few casual anastomoses, 3–6 per segment; sori lacking an indusiumlike scale, medial to supramedial, filiform scales present among the

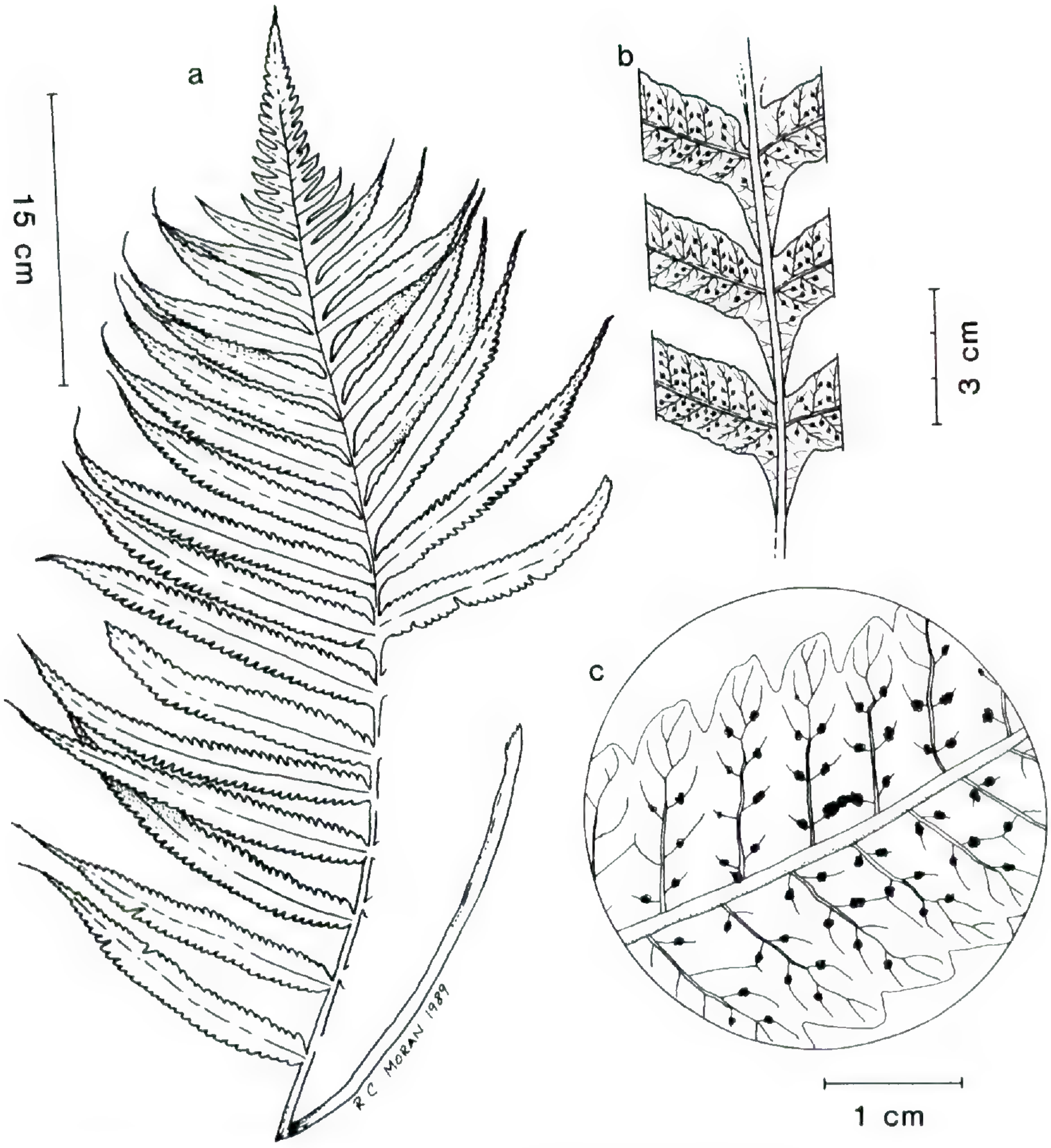
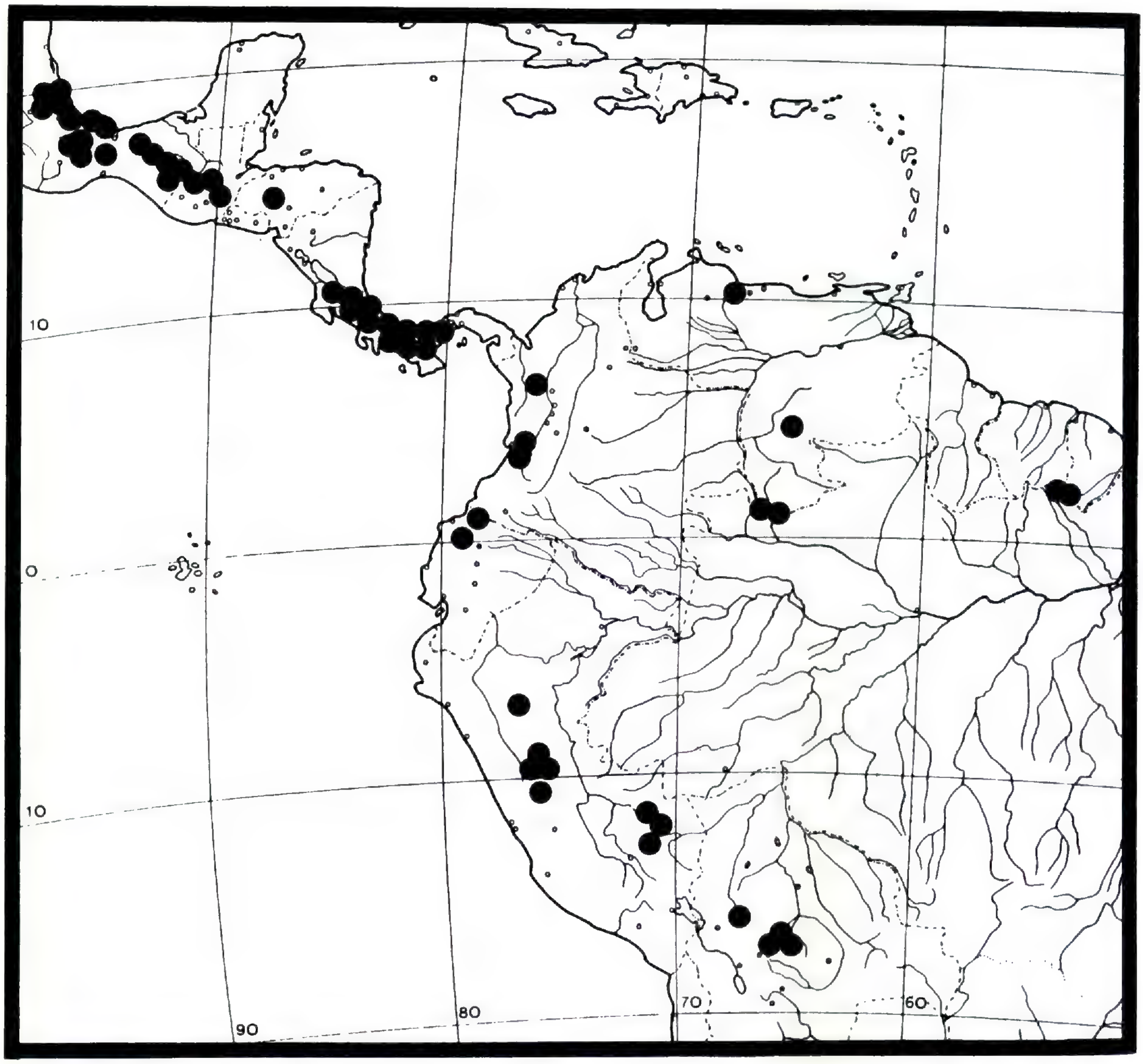


FIGURE 21. *Stigmatopteris longicaudata.*—a. Leaf (*Moran 3206*, MO).—b. Medial pinnae showing decurrent bases (*Liesner & Stannard 16909*, NY).—c. Venation and sori (*Moran 3206*, MO).

sporangia in plants from Venezuela, Peru, and Bolivia.

Additional specimens examined. MEXICO. CHIAPAS: 10 km above Rayón Mezcalapa along road to Jitotol, Municipio of Rayón, 1,700 m, *Breedlove & Smith 32672* (F, MICH, NY); Monte Bello National Park, Municipio of La Trinitaria, 1,300 m, *Breedlove 35128* (F, MO); E of Laguna Tzikaw, Monte Bello National Park, Municipio of La Trinitaria, 1,300 m, *Breedlove 35028* (MICH, MO, NY); 10 km ENE of Dos Lagos above Santa Elena, Municipio of La Trinitaria, 1,170 m, *Breedlove 56494* (MICH, MO, NY); near Ixtacomitan, 490 m, *Rovirosa 822* (K, PH). OAXACA: Dtto. Villa Alta, valley of the Yelagago River, ca. 20 mi. NE of Villa Alta, *Mickel 975* (MICH, US), 2,072 m, *990* (MICH, US); Dtto. Ixtlán, 79 km N of Ixtlán de Juárez on Rte. 175, 1 km S of Campamento Vista Hermosa, 1,100–1,200 m, *Mickel 5662* (NY, UC, US); Dtto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, ca. 500–600 m, *Mickel 6369* (NY); 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, *Mickel 6392* (NY); Dtto. Ixtlán, 7 km S of Vista Hermosa, 71 km N of Ixtlán de Juárez on Rte. 175, 1,645 m, *Mickel & Pardue 6727* (NY); Dtto. Ixtlán, 2–3 km S of Vista Hermosa, 75–76 km N of Ixtlán de Juárez on Rte. 175, 1,615 m, *Mickel & Pardue 6543* (NY, UC); road from Oaxaca to Tuxtepec, km 125–153, *Hellwig 491* (NY), *492* (NY), *494* (NY); Ixtlán–Tuxtepec road, 35–39 km S of Valle Nacional, km 96–100, *Mickel 1523* (MICH, NY, US); hwy. through Sierra de Juárez between Tuxtepec and Oaxaca, 21.5 mi. S of bridge at Valle Nacional, S of La Esperanza, 1,660 m, *Croat 48097* (CR, MO); 47 mi. from Ixtlán on Rte. 175, *McAlpin 1043* (DUKE); Dtto. Tehuantepec, along Continental Divide between La Chiguzhe and Guevea de Humboldt, ca. 1,200 m, *Hallberg 1724* (NY). PUEBLA: Limonateno, Municipio de Hueytamalco, 1,000 m, *Mickel 484* (MICH), *Ventura A. 484* (NY). VERACRUZ: 6 km by road N of Paz de Enríquez, Municipio Yecuatla, 1,200 m, *Nee et al. 26382* (F, NY, Z); Plan de Almansa, Municipio de Yecuatla, 600 m, *Ventura A. 3306* (CR, NY); Lomas de Santa Rita, Municipio de Yecuatla, *Ventura A. 3630* (NY); camino Bastonal a Santa Marta, Municipio Catemaco, *Gómez-Pompa et al. 5457* (F); La Calavera, 5 km adelante de Atalen, Municipio de Atzalan, *Calzada 5212* (F); 9 km E of Tebanca (9 km E of Lago Catemaco), 980 m, *Nee & Schatz 19868* (F); 12 km S of Misantla, 1,350 m, *Bohs et al. 1704* (GH); ca. 8 km



MAP 6. Distribution of *Stigmatopteris longicaudata*, the most widely distributed species in the genus.

S of Misantla, ca. 750 m, *Conant 792* (GH), *Barrington 410* (GH); Santa Rita prope Misantla, *Hahn 352* (MO, P); Cordova, *Finch 169* (UC). GUATEMALA. ALTA VERAPAZ: Hochwald bei Purulhá, 1,800 m, *von Türckheim 111691* (GH, NY, P, US). BAJA VERAPAZ: Salama, Aldea San Rafael Chilasco, *Guzmán-Valdez 892* (F); Hochwald in Pauyal, 1,350 m, *von Türckheim 3865* (GH, US). HUEHUETENANGO: vic. of Maxbal, 17 mi. N of Barillas, 1,500 m, *Steyermark 48744* (F, US); Cerro Negro, 2 mi. E of Las Palmas, 1,600–2,000 m, *Steyermark 51710* (F, US). HONDURAS. COMAYAGUA: hills above Varsovia, near town of Cerro Azul, 900 m, *Hazlett 3029* (MO). COSTA RICA. ALAJUELA: ca. 20 km N of San Ramón, at the Univ. of San Ramón's Biological Field Station, cloud forest, 1,100 m, *Moran 3206* (CR, F, GH, MO); Monteverde Cloud Forest Reserve, 1,520–1,580 m, *Dryer 366* (F); Monte Verde Reserve, Atlantic slope in valley or Río Peñas Blancas, 900–950 m, *Hammel et al. 14238* (MO). CARTAGO: ca. 10 km SE of Tapantí, *Wilbur & Stone 8919* (DUKE); 16 km S of Tapantí, *Stolze 1487* (CR, F, UC); Tapantí, 1,300–1,800 m, *Gómez 18778* (CR, MO, PORT, UC); Tapantí, Quebrada Valverde, *Gómez & Wagner 6856* (CR); Tapantí Hydroelectric Reserve, 1,500 m, *Croat 36176* (CR, MO); along tributary of Quebrada Casa Blanca Tapantí, 1,350 m, *Grayum & Sleeper 3683* (MO, UC); trail leading E into mountains from road into Tapantí Reserve, ca. 1 km S of jct. of Quebrada Salto and Río Grande de Orosi, 1,500–1,800 m, *A. R. Smith et al. 2194* (CR, MO, UC); ca. 15 km S of Tapantí along the new road, on the E slope above the Río Grande de Orosi near the concrete bridge, 1,500 m, *Burger & Liesner 6773* (CR, F, GH). HEREDIA: Estación Biológica La Selva, at confluence of Río Sarapiquí and Río Puerto Viejo, Atlantic slope, 50–80 m, *Grayum et al. 7910* (DUKE, MO); vic. of La Palma, on the road to La Hondura, 1,500–1,700 m, *Maxon & Harvey 8075* (US); Sardinal, 1,600 m, *Gómez 2182* (CR, F, GH, NY, UC, US); area between Río Peje and Río Ardinalito, Atlantic slope of Volcán Barva, 480–520 m, *Grayum 6893* (MO); Zona Protectora, N slopes of Volcán Barba, between Río Peje and Río Guacimo, along Quebrada Cantarana, 190 m, *Grayum & Schatz 3089* (DUKE); Zona Protectora-Q, Canta Rana Magsasay, 400 m, *Chacón 852* (CR). SAN JOSÉ: along unnamed N fork of Río Zurqui, 1,500–1,600 m, *A. R. Smith et al. 1678* (MO, NY, UC). PANAMA. BOCAS DEL TORO: vic. of Cerro Colorado, on trail along creek

8.6 mi. from Camp Chami, 1,400 m, *McPherson 8885* (MO, UC); Cerro Colorado, ca. 8.6 mi. W of Chamé, *Croat 69108* (MO, NY, PMA, UC, US); along road between Fortuna Dam and Chiriquí Grande, 8.5 km N of bridge, 4.3 km N of Continental Divide, *Croat & Grayum 60177* (MO, UC); along road between Fortuna Dam and Chiriquí Grande, 7.3 mi. N of bridge, 3.2 mi. N of Continental Divide, 700 m, *Croat & Grayum 60215* (MO). CHIRIQUÍ: vic. of Cerro Colorado mine above San Felix, 1,450 m, *McPherson 12035* (MO); above Boquete, on trail to Pate Macho on Continental Divide, 1,850–2,100 m, *McPherson 12310E* (MO); Canassa, 2,500 m, *Killip 5444* (US). COCLÉ: El Valle, *González 14* (MO); La Mesa, above El Valle de Antón, ca. 2 km W of Cerro Pilon, 900 m, *Croat 37492* (MO, US); upper Caldera watershed, between "Camp I" and the divide, Holcomb's trail, above El Boquete, 1,650–1,925 m, *Maxon 5647* (NY, US); Holcomb's Trail, above El Boquete, 1,675–1,800 m, *Killip 5344* (GH, US). VERAGUAS: Cerro Tute, ca. 2 km N of Santa Fé, 900–1,100 m, *Moran 4048* (MO, STRI, UC); along Río Dos Bocas, ca. 12 km beyond Santa Fé, 450 m, *Croat 25818*, (MO), *27736* (MO); 11 km from Escuela Agrícola Alto Piedra on road to Calovebora, 450 m, *Croat 27541* (MO); 5 mi. W of Escuela Agrícola Alto Piedra, 800–1,200 m, *Croat 22998* (MO, NY); area of Santa Fé, road past Escuela Agrícola Alto Piedra, 700 m, *Churchill et al. 5984* (MO, UC). FRENCH GUIANA. Tumuc Humac, à mi-chemin entre le Mitaraka Sud et le Toukouchipann, 480 m, *de Granville 1291* (Z); Tumuc Humac, au SE du Mitaraka Sud, 400 m, *de Granville 1434* (NY, P, Z). VENEZUELA. CARABOBO: las laderas arriba de las cabeceras de Río San Gián, E de Los Tanques, S de Borburata, 750–1,100 m, *Steyermark & Steyermark 95406* (GH, VEN). TERRITORIO DE AMAZONAS: Depto. Atures, lower forested E slope of 1,760 m peak, 8 km NW of settlement of Yutuje, 3 km W of Río Coro-Coro, W of Serranía de Yutaje, 1,050–1,200 m, *Liesner & Holst 21882* (MO, UC); Depto. Río Negro, Cerro de Neblina Camp V., valley north base of Pico Cardona, 1,250 m, *Liesner & Stannard 16909* (F, MO, NY, UC, US); Cerro de Neblina, Río Yatua, 5–8 km S of Camp 3, 1,100–1,600 m, *Maguire et al. 36864* (F, MICH, NY). COLOMBIA. ANTIOQUIA: Municipio de Frontino, road between Nutibara and La Blanquita, region of lower Murri, ca. 28 km from Nutibara, 960 m, *MacDougal et al. 3811* (MO, UC). EL VALLE: Cordillera Occidental, vertiente occidental, Hoya del Río Digua, lado derecho, La Elsa, quebrada La Cristalina, 1,000–1,150 m, *Cuatrecasas 15240* (F, US); Cordillera Occidental, vertiente occidental, Hoya del Río Digua, lado izquierdo, Piedra de Moler, 900–1,180 m, *Cuatrecasas 15122* (F, US). ECUADOR. PICHINCHA: NE of Vicente Maldonado, Reserva de ENDESA, 600 m, *Laegaard 52431* (AAU, MO). CARCHI: wet plateau above San Marcos de los Coaiqueres, trail toward Gualpí Bajo, 1,000 m, *Øllgaard et al. 57515* (AAU, MO). PERU. CUZCO: Province Paucartambo, Cosñipata Valley, Río Tono, first foothill ridge on road N of Patria, 800 m, *Wachter et al. 200* (F). HUÁNUCO: Tingo María, 700 m, *Tryon & Tryon 5330* (BM, F, GH). JUNÍN: E of Quimirí Bridge, near La Merced, 800–1,300 m, *Killip & Smith 23906* (NY, US); ridge E of Tingo María, 625–1,100 m, *Allard 22558* (US). MADRE DE DIOS: Province Manú, Cerro de Pantiacolla, Río Palotoa, 10–15 km NNW of Shintuya, transect to ridge top, 700–1,000 m, *Foster et al. 10908* (F); Parque Nacional del Manú, Cocha Cashu Biological Station, *Foster P-84-91* (F). SAN MARTÍN: Mt. Guayrapurima, near Tarapoto, *Spruce 4012* (BM, G, K, P). UCAYALI: Province Coronel Portillo, Sinchono, cerca de la Divisoria, 1,500 m, *Aguilar 861* (GH, USM); Sinchono, entre Tingo María y Pucallpa, 1,500 m, *Aguilar 865* (GH). BOLIVIA. COCHABAMBA: Province Carrasco, Antahuacana, Quebrada Espiríto Santo, 750 m, *Buchtien 64* (P), *2166* (BM); Province Carrasco, confluencia del Río Leche con el Río Isarsama, 220 m, *Beck 1625* (UC). LA PAZ: región de Mapiri, San Carlos, 850 m, *Buchtien 233* (GH, MO, UC, US); San José de Mapiri, 750 m, *Cardénas 1020* (GH); Province Nor Yungas, 13 km NE del camino entre Yolosa y Caranavi, por el camino a Suapi, al lado del Río Khusillani, ca. 1 km antes la comunidad Khusillani, 1,500 m, *Solomon 18469* (MO).

Stigmatopteris longicaudata occurs from Mexico to French Guiana and Bolivia (Map 6), 220–2,100(–2,500) m, and is the most widely distributed species in the genus. Its most distinctive features are the pinnae, which are less lobed than most other species and, at least in the distal part of the lamina, have long-decurrent bases (Fig. 21b). The specimens from Peru and Bolivia differ from the rest by the linear and fibrillose scales (vs. ovate-lanceolate) on their axes and veins. No other difference correlates with scale type.

15. Stigmatopteris michaelis (Baker) C. Chr., Bot. Tidssk. 29: 300. 1909. *Polypodium michaelis* Baker, J. Bot. 6: 164. 1877. TYPE: Ecuador. Pichincha: near Santo Domingo de los Colorados, *Sodiro 2615* (holotype, K; isotypes, P, Q, SI). Figure 22. Map 7.

Polypodium sylvicola Baker, J. Bot. 19: 205. 1881. *Dryopteris sylvicola* (Baker) C. Chr., Index Filic. 297. 1905. TYPE: Colombia. Antioquia: 1,000 m, *Kalbreyer 1807* (holotype, K).

Rhizome short-creeping; leaves 30–70 cm; petioles ⅔ to equaling the lamina, the base dull brown, becoming stramineous distally, scaly, the scales opaque, black, appressed, or membranous, tan, and spreading; leaves 0.3–0.7 m long; lamina 1-pinnate-pinnatifid, winged for ⅔–¾ the length, narrowly deltate to lanceolate, the apex evenly attenuate; pinnae (4.5–)9–11 × (1–)1.8–2.2 cm, pairs 17–20, widest at or slightly above the middle, lobed ca. halfway to the costa, the base of the distal pinnae adnate and decurrent, the base of the basal pinnae stalked, the stalk 1–3 mm; rachis and costae stramineous, scaly, the scales scattered; less than 0.4 mm, filiform, the larger ones with several cilia at their base; veins free, unbranched, (3–)4–6(–7) per segment; sori lacking an indusiumlike scale, paraphysate, the paraphyses ca. equaling the sporangia, uniseriate, multicellular, dark brown, spreading, somewhat tortuous.

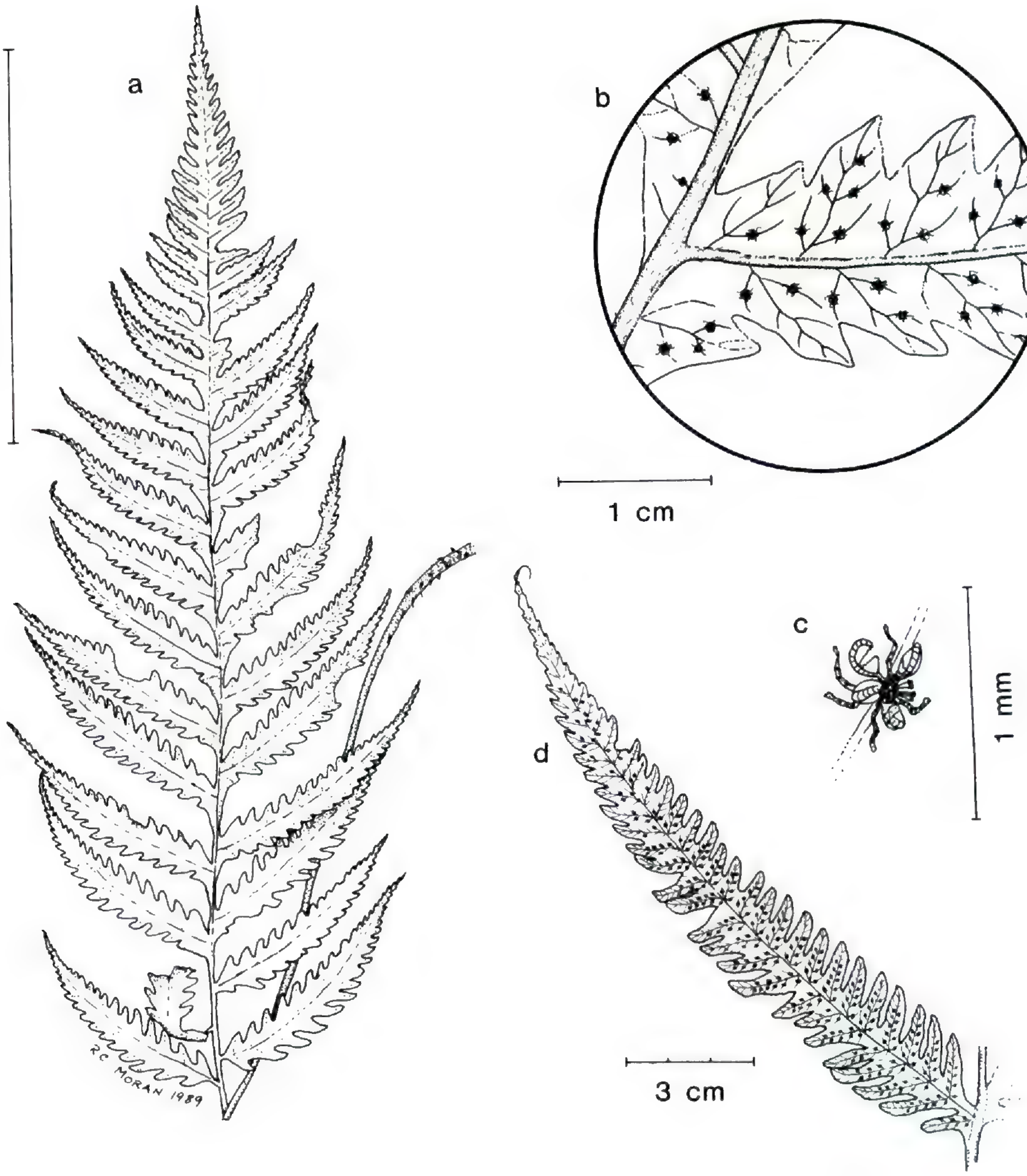


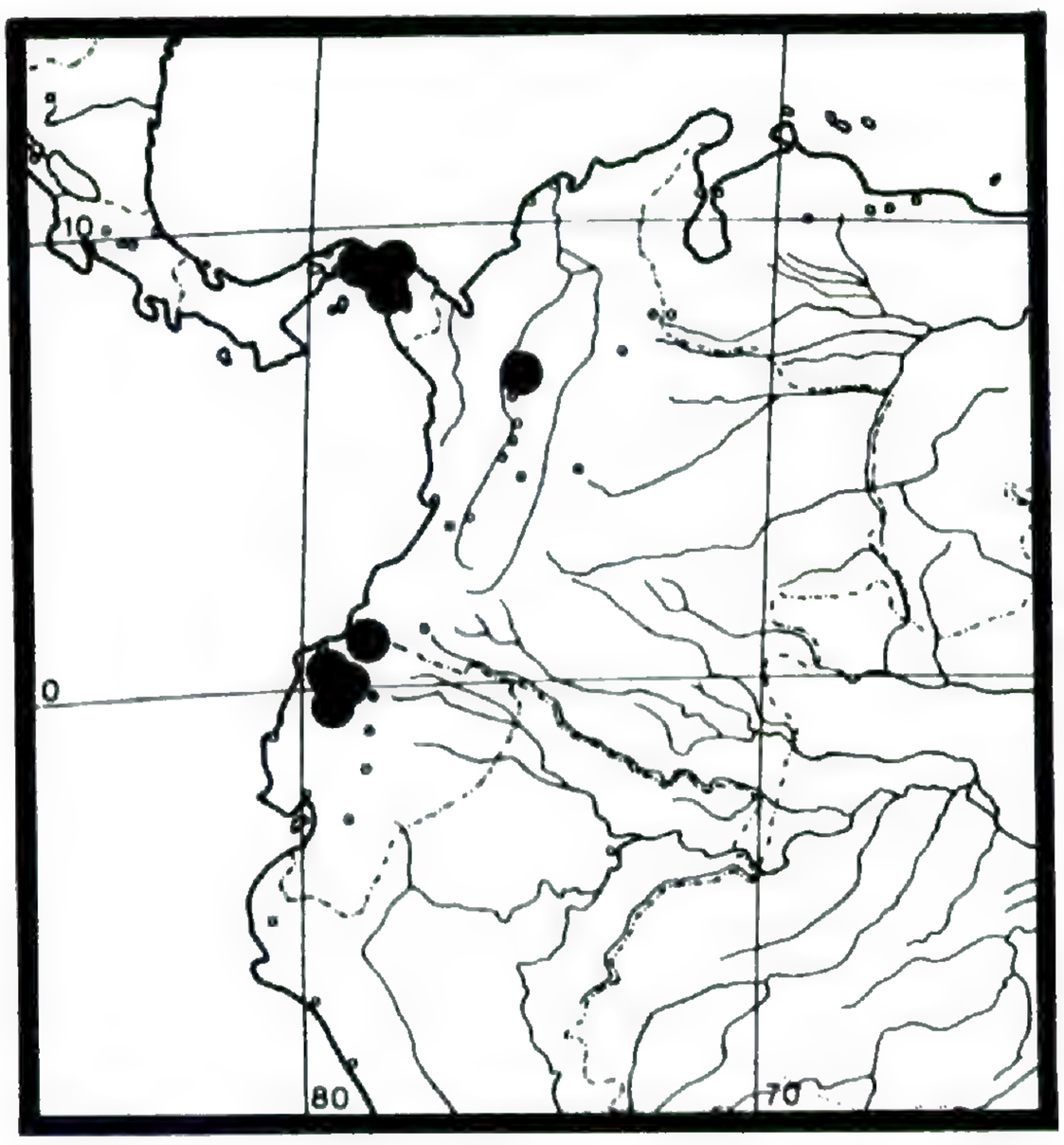
FIGURE 22. *Stigmatopteris michaelis.*—a. Leaf.—b. Base of medial pinnae.—c. Paraphysate sorus.—d. Medial pinna. a, b, *McDonough et al. 371*, MO. c, d, *Sodiro s.n.*, UC.

Additional specimens examined. PANAMA. PANAMÁ: Cartí road, ca. 15 km from its beginning, 300 m, *Hammel & Kress 13398* (DUKE, F, MO, US). COMARCA DE SAN BLAS: trail along continental divide, 400 m, *McDonough et al. 371* (MO); Nusagandi, El Llano–Cartí road, 350 m, *van der Werff 7010* (MO, NY, UC). ECUADOR. CARCHI–ESMERALDAS: Lita, 600 m, *van der Werff et al. 9566* (MO). PICHINCHA: in silvis tropical prope San Miguel, 1882, *Sodiro s.n.* (UC); NE of Vicente Maldonado, Reserva de ENDESA, 600 m, *Laegaard 52224*, (AAU).

Stigmatopteris michaelis occurs from Panama to Ecuador (Map 7) on steep clay banks along streams, from 300 to 1,000 m. It is distinctive by the combination of long-decurrent pinna bases, pinnae lobed about halfway to the costa, and paraphysate sori (Fig. 22). The paraphyses are easily overlooked because they resemble stalks of the sporangia, but they can be distinguished by their darker color, slightly tortuous habit, and one-celled (not three-celled) apex. In general, *S. michaelis* has a smaller leaf than other species in the genus. The derivation of the specific epithet is unknown.

16. Stigmatopteris nephrodioides (Klotzsch) C. Chr., Bot. Tidsskr. 29: 299. 1909. *Polypodium nephrodioides* Klotzsch, Linnaea 20: 384. 1847. TYPE: Venezuela, *Karsten 9, Coll. II* (holotype, B). Figure 23. Map 8.

Rhizome short, ascending; leaves to 2 m; petioles ca. ½ to equaling the lamina, tan to brown, the scales 3–13 × 1–2 mm, lanceolate, entire; lamina 1-pinnate-pinnatifid, lanceolate, bulblets lacking;



MAP 7. Distribution of *Stigmatopteris michaelis*.

pinnae 18–25 × 2.1–3.5 cm, cut ¼–½ to the costa, or rarely more in enlarged basal pinnae, the basal ones stalked, the distal ones gradually becoming sessile, then adnate, the basal basiscopic lobe of the medial pinnae often overlapping the rachis, the basal acroscopic lobe often prolonged; rachis and costae moderately scaly, the scales lanceolate; lobes rounded, entire; veins 4–8 per lobe, unbranched; sori lacking an indusial scale.

Additional specimens examined. VENEZUELA. ANZOÁTEGUI: Cerro Peonía (Cerro Coroy), above Carmelita, between Río León and Bergantín, NE of Bergantín, 1,000–1,450 m, *Steyermark 61403* (F). ARAGUA: along road between Colonia Tovar and Carayaca, 2.3 km below the junction with Colonia Tovar–Caracas road, 750 m, *Croat 54475* (MO, UC); along road between Maracay and Ocumare de la Costa, Henri Pittier National Park, 3 km N of summit, 970 m, *Croat 60576* (NY, UC); near Colonia Tovar, *Fendler 198* (BM, G, GH, K, MO, P, US), *Funck & Schlim 411* (BM, G, P); cloud forests of the valle de Ocumare, 1,100 m, *Pittier 12172* (US, VEN); Parque Nacional Henry Pittier, above Guamitas, along trail to La Mesa, *Steyermark 89747* (GH, US); Cordillera Interior, entre El Pauji y El Socorro, hacia la represa, S de El Consejo, 1,350–1,400 m, *Steyermark & Stoddart 118173-A* (GH, VEN). CARABOBO: ca. 18–20 km S of Puerto Cabello, ca. 9–14 km S of San Esteban on old trail to Valencia, 0–4 km S of colonial bridge, 350–700 m, *Liesner & Medina 13739* (MO, UC, VEN); arriba de las cabeceras del Río San Gián, E de Los Tanques, S de Borburata, *Steyermark & Steyermark 95406-A* (F, GH, NY, US, VEN). DISTRITO FEDERAL: old road between Portachuelo and Peñita (Petaquire and Carayaca), between Colonia Tovar–Junquito road and Hacienda El Limon, 6–8 mi. below junction of Junquito–Colonia Tovar road, *Steyermark & Nevling 95914* (GH, NY, VEN). FALCÓN: Sierra de San Luis, arriba de Sta. María, 1,200 m, *van der Werff 3488* (MO, UC). MIRANDA: Dtto. Paéz, Fila La Tigra, Quebrada San Juan, 18 km SO de Cúpira, 650 m, *Ortega & González 369* (PORT, MO, UC). YARACUY: along road from Salom to Candelaria, 8–8.5 km above Salom Central Plaza, 1,260–1,290 m, *Croat 60765* (MO, NY, UC); Dtto. Bruzual, Montaña de María Lionza, Quebrada Quibayo, 250–1,000 m, *Steyermark et al. 125086* (UC); Cabeceras de la Quebrada Amparo, El Amparo hacia Candelaria, a 7–8 km N de Salom, 1,220–1,250 m, *Steyermark & Espinoza 111174* (NY, VEN); Dtto. Nirgua, El Amparo, 7–11 km N de Salom, 1,200–1,300 m, *Steyermark & Espinoza 111493* (NY, UC).

Stigmatopteris nephrodioides is endemic to north-central Venezuela (Map 8), where it occurs in wet forests from 650 to 1,450 m. A good character to identify this species is the basal basiscopic lobe of the medial pinnae that overlaps the rachis (Fig. 23a). The only other species of *Stigmatopteris* with pinna bases that overlap the rachis is *S. contracta*, a Costa Rican species that differs greatly in leaf cutting (Fig. 12). The name *S. alloëoptera* (Kunze) C. Chr. may apply to *S. nephrodioides*, but I have not seen the type and therefore cannot be certain (see section on names of uncertain application).

17. Stigmatopteris opaca (Baker) C. Chr., Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk. Afd. ser. 7, 10: 78. 1913. *Meniscium opacum* Baker, J. Bot. 15: 166. 1877. *Phegopteris opaca* (Baker) Christ, Farnkr. Erde 270. 1897, illegit., non (Sprengel) Mett. 1858. *Dryopteris christii* C. Chr., Index Filic. 257. 1905, a nom nov. for *Meniscium opacum* with the same type, non *Dryopteris opaca* (Don) C. Chr. 1905. TYPE: Ecuador. *Sodiro 54/3* (holotype, K; isotypes, P, UC; photos, BM, GH, US ex K). Figure 24. Map 8.

Polypodium oligophlebium Baker in Hook. & Baker, Syn. Fil. 506. 1874, hom. illeg., non Kunze 1850. *Phegopteris oligophlebia* Salomon, Nomencl. 276. 1883, nom. nov. for *Polypodium oligophlebium* Baker, with the same type. *Dryopteris paucinervata* C. Chr., Index Filic. 283. 1905, a nom. nov. for *Polypodium oligophlebium* Baker, with the same type. TYPE: Peru. San Martín: Tarapoto, *Spruce 4653* (holotype, K).

Polypodium coalescens Baker, J. Bot. 15: 164. 1877. *Dryopteris coalescens* (Baker) C. Chr., Index Filic. 258. 1905. TYPE: Ecuador. Pichincha: near San Miguel de los Colorados, Aug. 1875, *Sodiro 54/2* (holotype, K).

Rhizome erect, the internodes approximate, scaly at the apex, the scales 1–3 mm, lanceolate, opaque, brown, rigid, entire; leaves to 1 m; petiole ½ to equaling the lamina, dull brown on both surfaces, scaly, the scales of two types, the smaller type 2–5 mm, opaque, appressed, shiny black abaxially,

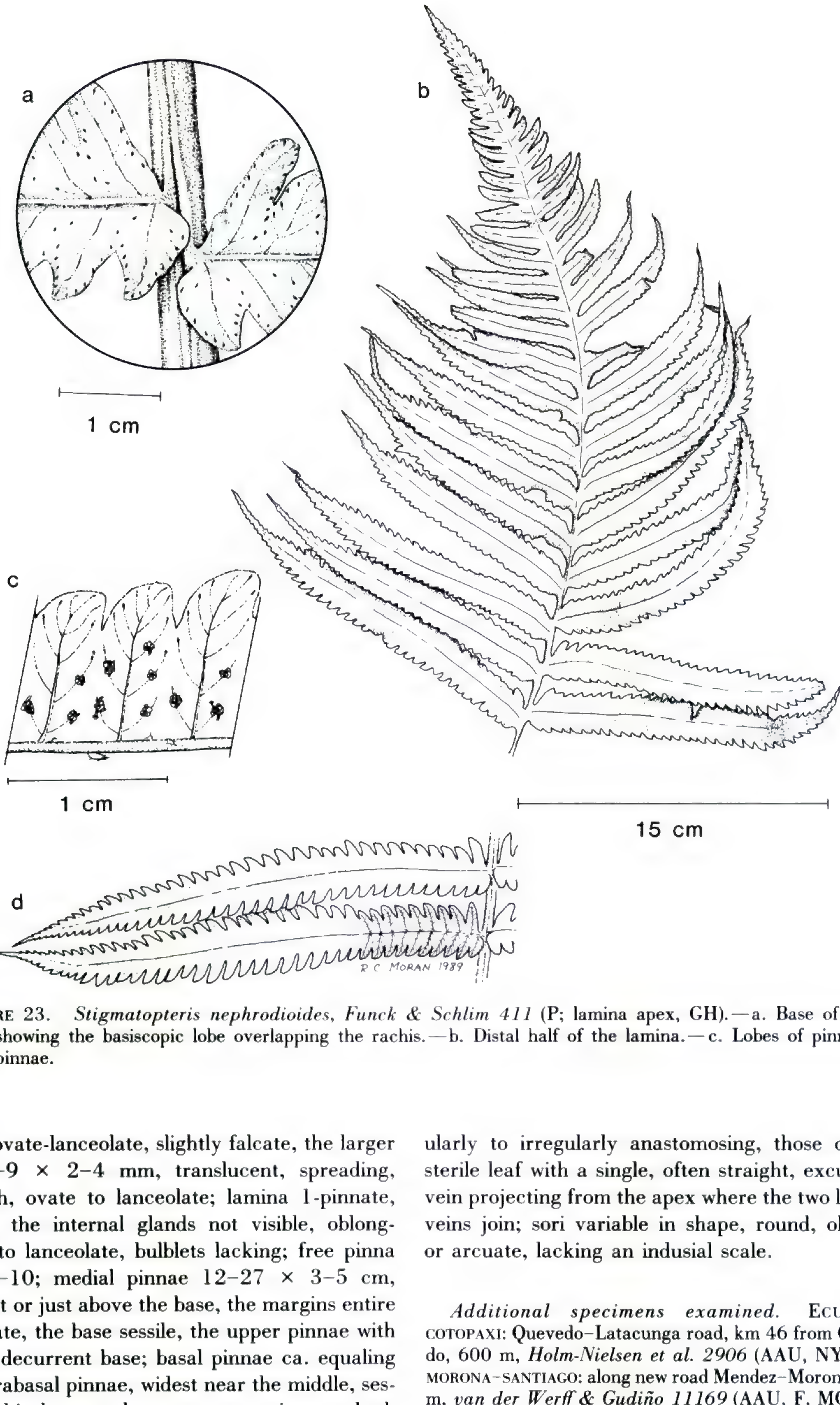
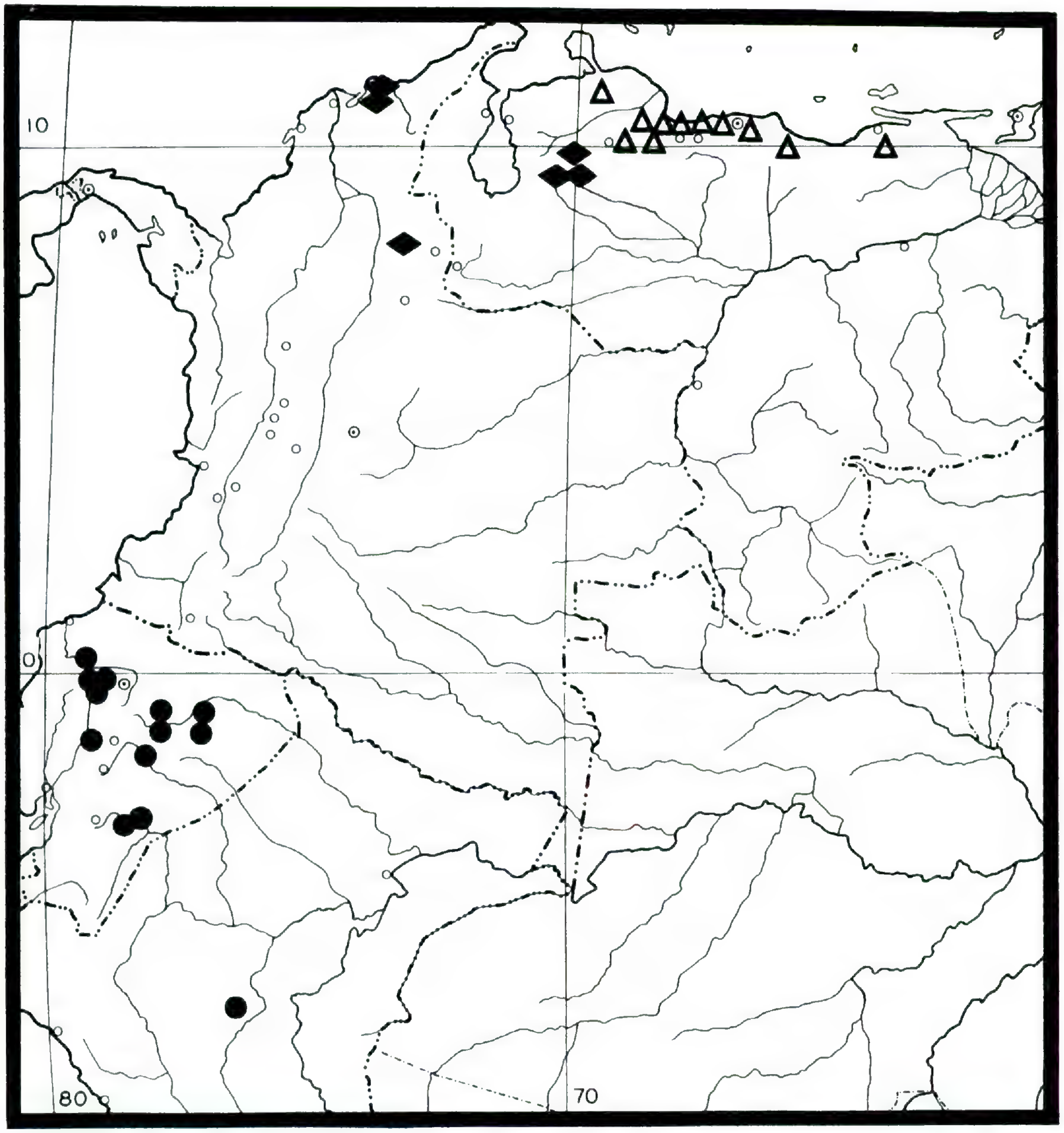


FIGURE 23. *Stigmatopteris nephrodioides, Funck & Schlim 411* (P; lamina apex, GH).—a. Base of medial pinnae showing the basiscopic lobe overlapping the rachis.—b. Distal half of the lamina.—c. Lobes of pinna.—d. Medial pinnae.

entire, ovate-lanceolate, slightly falcate, the larger type 4–9 × 2–4 mm, translucent, spreading, brownish, ovate to lanceolate; lamina 1-pinnate, opaque, the internal glands not visible, oblong-deltate to lanceolate, bulblets lacking; free pinna pairs 4–10; medial pinnae 12–27 × 3–5 cm, widest at or just above the base, the margins entire to crenate, the base sessile, the upper pinnae with a short decurrent base; basal pinnae ca. equaling the suprabasal pinnae, widest near the middle, sessile; rachis brown, the costae stramineous, both axes lacking capitate-glandular hairs, scaly, the scales lanceolate to linear or amorphous; veins regularly to irregularly anastomosing, those of the sterile leaf with a single, often straight, excurrent vein projecting from the apex where the two lateral veins join; sori variable in shape, round, oblong, or arcuate, lacking an indusial scale.

Additional specimens examined. ECUADOR. COTOPAXI: Quevedo–Latacunga road, km 46 from Quevedo, 600 m, *Holm-Nielsen et al. 2906* (AAU, NY, UC). MORONA–SANTIAGO: along new road Mendez–Morona, 650 m, *van der Werff & Gudiño 11169* (AAU, F, MO, NY, UC). NAPO: Cordillera Guacamayos, on road Baeza–Tena, ca. 34 km from Baeza, ca. 2,000 m, *Øllgaard et al. 35859* (AAU); vic. of Jaguar Hotel, Río Napo, *Proctor*



MAP 8. Distribution of *Stigmatopteris opaca* (dots), *S. pterorhachis* (diamonds), and *S. nephrodioides* (open triangles).

38712 (NY); ca. 10 km SE of Coca, 250 m, *Harling et al. 19737* (UC); camino entre Puyo–Tena, casi 10 km S de Río Napo, 500 m, *Moran 3576* (MO, QCA). PASTAZA: 2 km W of Yuralpa, 440 m, *Holm-Nielsen & Jeppesen 992* (AAU, NY); Pastaza Canton, 20 km al sur de la población de curary, *Zak & Espinoza 5287* (MO, QCNE). PICHINCHA: near San Miguel, *Sodiro s.n.*, Jan. 1882 (P, US); Peripa flumine, 300–400 m, *Verleysen 174* (P); flumen Peripa, Toachi, *Sodiro s.n.* (SI); NE of Vicente Maldo, Reserva de ENESA, 600 m, *Laegaard 51614* (AAU, MO). ZAMORA–CHINCHIPE: ca. 4 km. E Paquisha, 1,250 m, *Øllgaard et al. 90435* (AAU, MO).

Stigmatopteris opaca occurs in Ecuador and Peru (Map 8), from 250 to 2,000 m. It is extremely variable in venation and shape of the sori. Although the veins are always anastomosing, they may do so irregularly (as in the other species with anastomosing veins) or they may do so regularly, with the veinlets straight and producing a single excurrent veinlet where they unite. This latter type of venation is similar to that found in *Thelypteris* subg. *Meniscium*. The sori vary from round to (in the type) arcuate, but some intermediate specimens have shapes between these extremes (Fig. 24b, c, e).

This species may be distinguished from *S. heterophlebia* by its nonpubescent axes and greater number of pinna pairs. It can be distinguished from

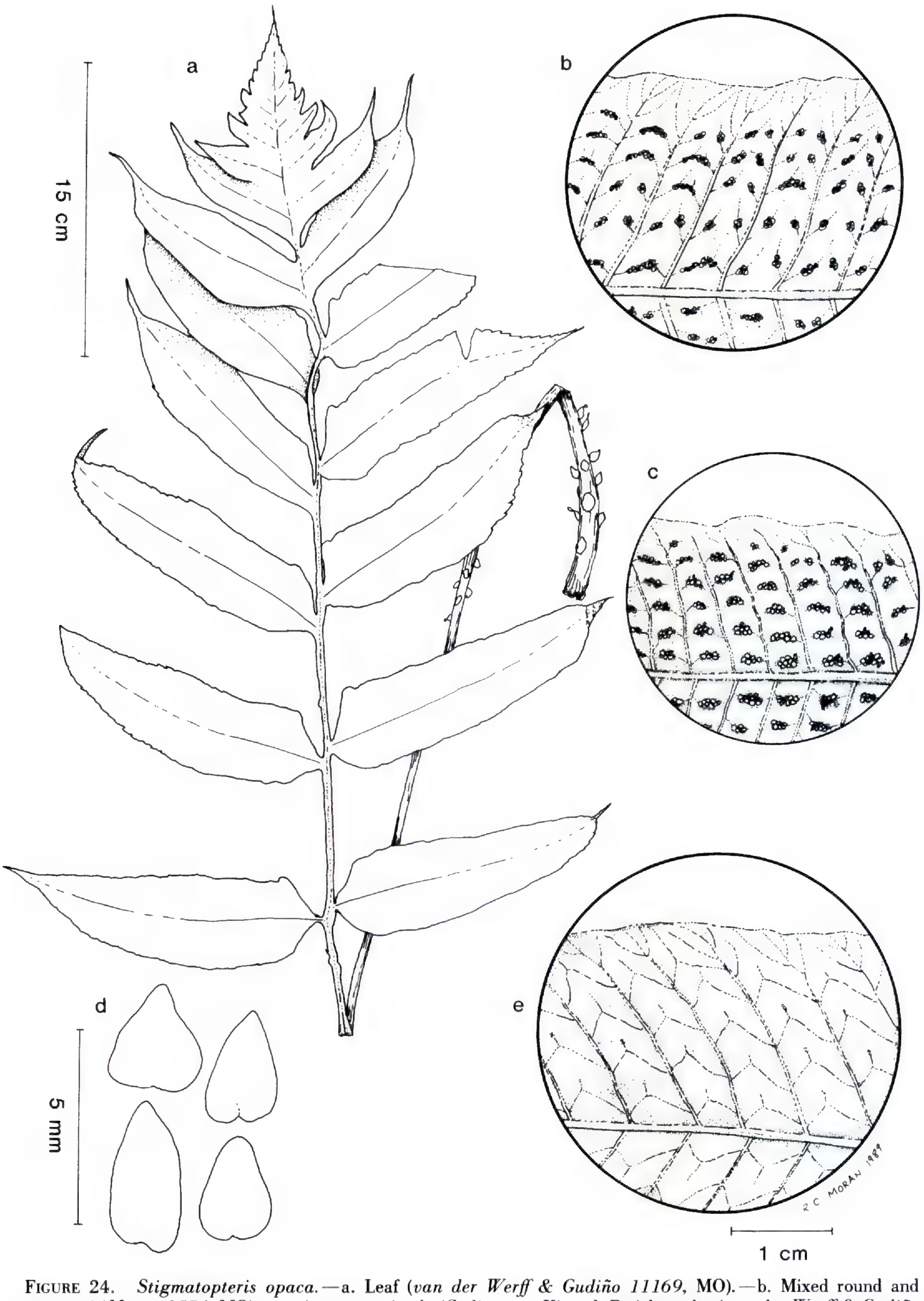
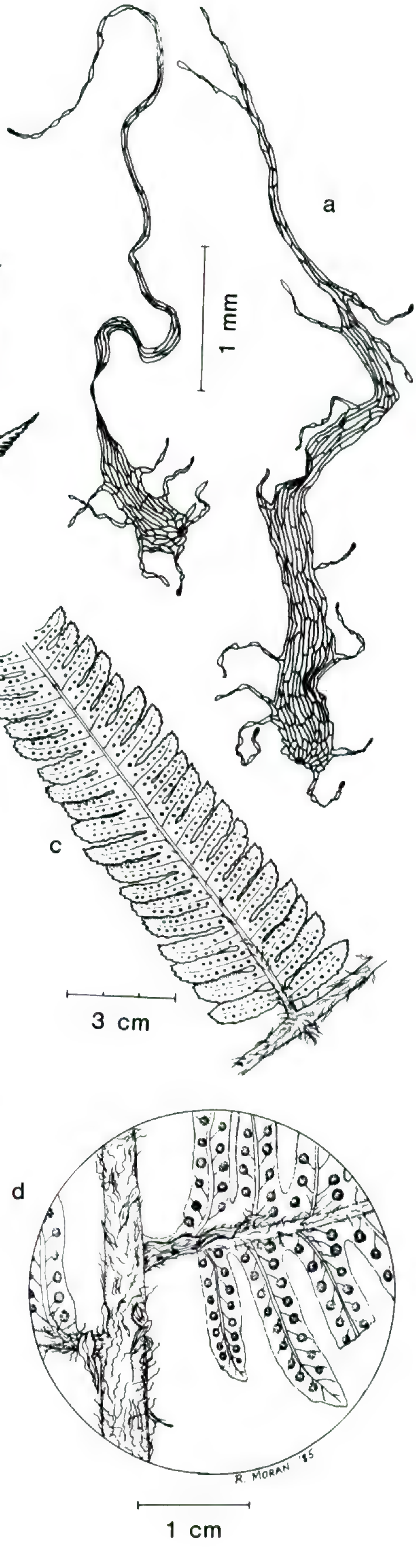


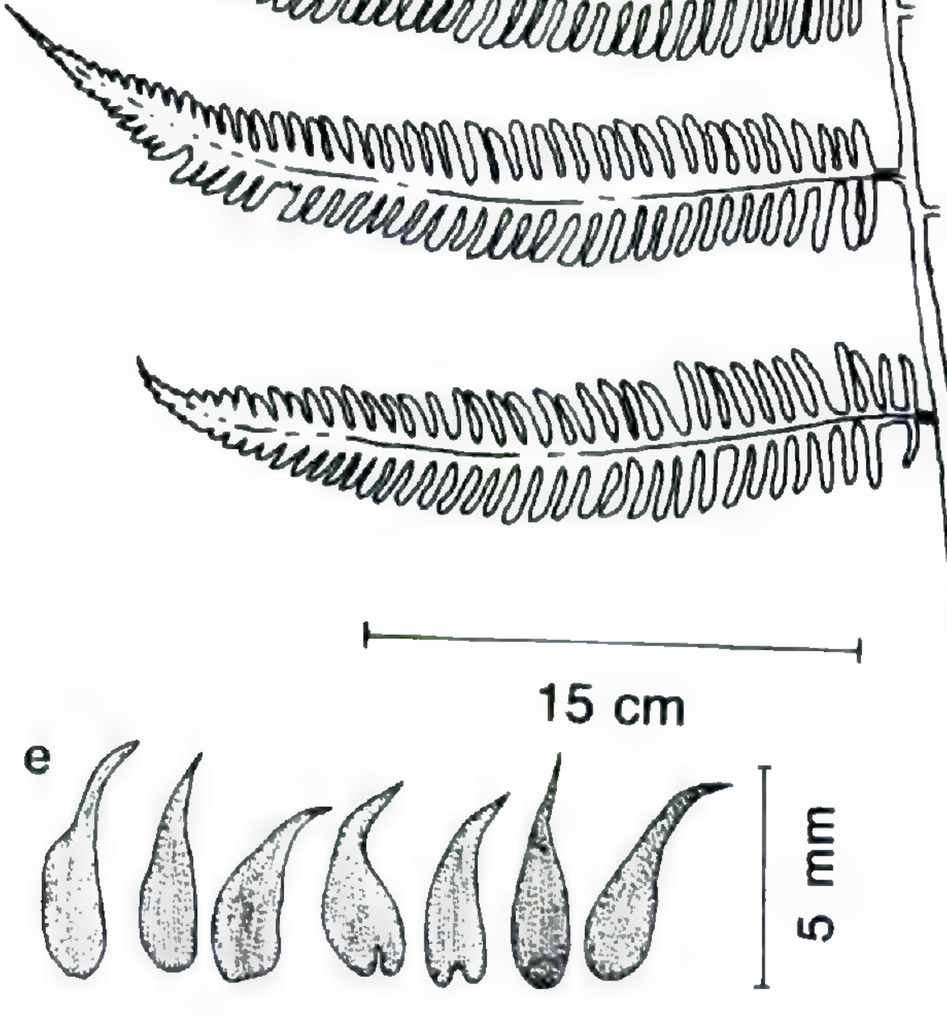
FIGURE 24. *Stigmatopteris opaca.*—a. Leaf (*van der Werff & Gudiño 11169*, MO).—b. Mixed round and arcuate sori (*Moran 3576*, MO).—c. Arcuate sori only (*Sodiro s.n.*, K).—d. Petiole scales (*van der Werff & Gudiño 11169*, MO).—e. Venation of a sterile pinna, showing single excurrent veinlet from vein junctures (*Holm-Nielson et al. 2906*, AAU).

a
1 mm

b
15 cm


a
1 mm

c
3 cm


e
5 mm

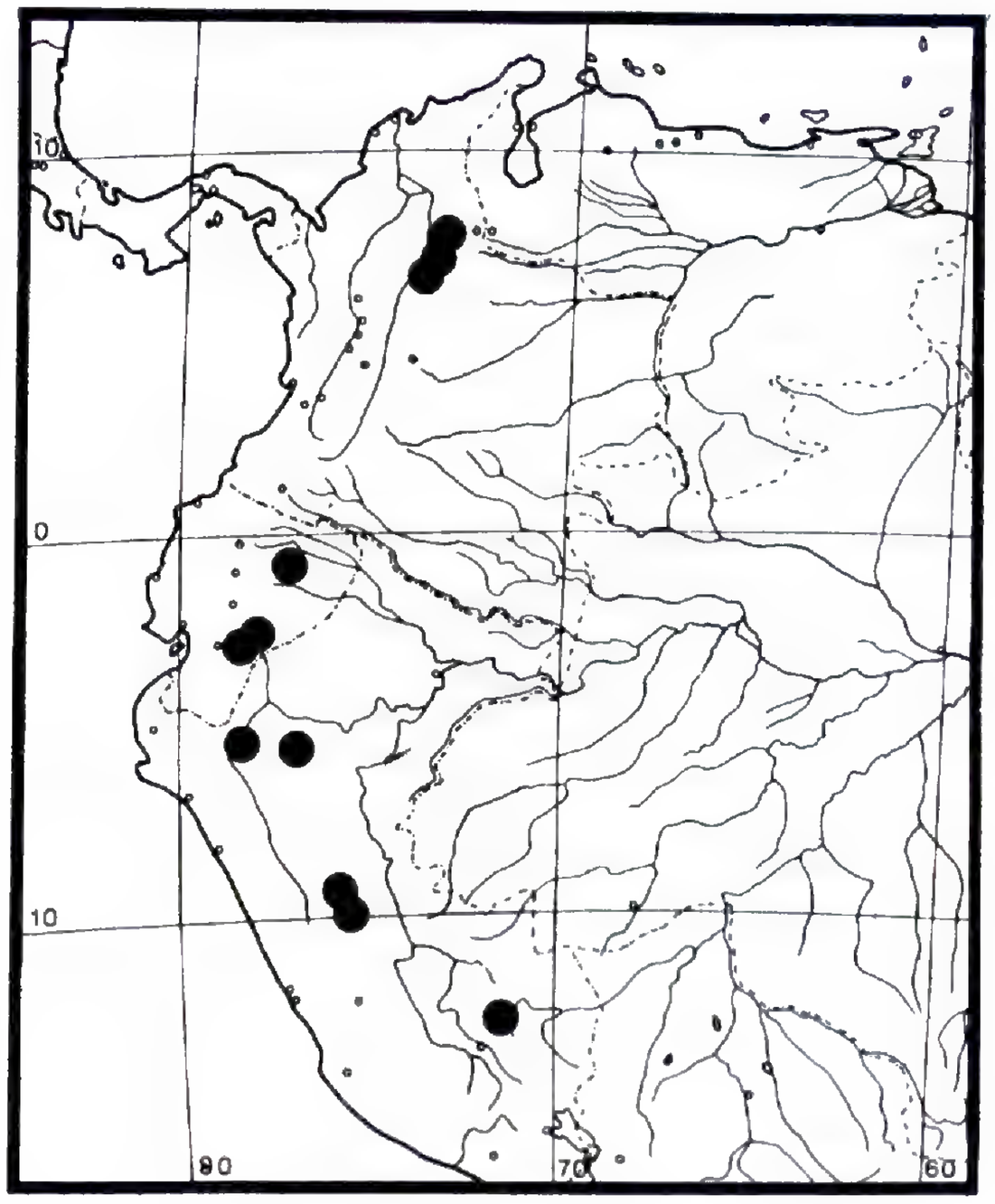
d
R. MORAN '85
1 cm

S. killipiana by its brown (not atropurpureous) petiole and rachis, thicker lamina, and tendency for the sori to become arcuate. The lamina is thicker and the glands less visible than in the other species of *Stigmatopteris*.

18. Stigmatopteris pellucidopunctata (C. Chr.) C. Chr., Bot. Tidsskr. 29: 304. 1909. *Polypodium macrophyllum* Hook., Sp. Fil. 4: 241. 1862, hom. illeg., non (Blume) Mett. 1856. *Phegopteris macrophylla* (Hook.) J. Smith, Hist. Fil. 233. 1875, hom. illeg., non Mett. 1859. *Dryopteris pellucidopunctata* C. Chr., Index Filic. 283. 1905, nom. nov. for *P. macrophyllum* Hook. TYPE: Peru. San Martín: Mt. Guayrapurima, Aug. 1856, *Spruce 4720* (holotype, K; isotypes, BM, G, P, US; photos, F, GH, MO, NY, UC ex BM). Figure 25. Map 9.

Rhizome erect or short-creeping; leaves to 2 m long; petiole ½ to equaling the length of the lamina, brown, scaly, the largest scales 4–6 × 2–2.5 mm, lanceolate, falcate, occasionally with darkly sclerified abaxial surfaces, the base cordate (appearing false peltate), with smaller fibrillose scales present, reddish; lamina 1-pinnate-pinnatifid, lanceolate, lacking buds; pinnae 20–40 × 2.5–6 cm, 15–20 pairs, cut ca. ⅔ to the costa, sessile or the basal ones short-stalked, the stalk 2–7 mm; segments 4–10 mm wide, serrate at the apex, the sides entire, serrate or rarely lobed, the basal basiscopic segment not reduced; rachis and costae stramineous or brown, scaly, the larger scales nonbullate, lanceolate to linear, mixed with smaller fibrillose ones; veins free, 7–14 per segment, unbranched or 1-forked with a short acroscopic branch that in fertile segments bears the sorus; sori lacking an indusiumlike scale.

Additional specimens examined. COLOMBIA. ANTIOQUIA: Municipio San Carlos, 47.5 km E of San Carlos, Lake Punchina, Quebradas La Villa y El Macho, *Brant et al. 1679* (MO). SANTANDER: ca. 25 km E of Puerto Wilches, E side of Magdalena Valley, 70–130 m, *Elias 8* (US); vic. of Barranca Bermeja, Magdalena Valley, between Sogamoso and Carare rivers, Amarilla Creek, 200 m, *Haught 1931* (GH, US). DEPTO. UNKNOWN: no locality, *Schlim 1683* (BM). ECUADOR. MORONA-SANTIAGO: along new road Mendez–Morona, 650 m, *van der Werff & Gudiño 11170* (MO, QCNE, UC). PASTAZA: Río Pastaza, between Destacamento Chiriboga and Apachi Entza, 285 m, *Øllgaard et al. 35212* (AAU). NAPO: 27 km SE of Coca, Pozo Auca 4, 200 m, *Moran 3624* (MO, Q, QCA). PERU. AMAZONAS: Provincia de Bagua, Quebrada Tambillo (below km 280 of Marañón road), valley of Río Marañón above Cascadas de Mayasí, 425–525 m, *Wurdack 2002* (GH, US, USM). HUÁNUCO: Fundo Chela, Sinchono, *Aguilar 927* (USM). MADRE DE DIOS: Provincia Manú, Atalaya, vic. of Hacienda Amazonia, 2–3 km W of village, 500–600 m, *Foster & Wachter 7437* (MO, USM). PASCO: Provincia Oxapampa, Paujil, near Puerto Bermúdez, *León et al. 311* (USM). BOLIVIA. LA PAZ: Provincia Sud Yungas, Chulumani, 107 km NNE pasando Asunta, Alto Charia sobre el Río San José afluente, Río Boopi, 900 m, *Beck 8500* (UC).



MAP 9. Distribution of *Stigmatopteris pellucidopunctata*.

Stigmatopteris pellucidopunctata grows from Colombia to Bolivia (Map 9), from 100 to 900 m. It is closely related to *S. sordida* and *S. ichthiosma* but may be distinguished by linear to fibrillose scales on the costae and costules (Fig. 25a). The stiff, adaxially sclerified, appressed petiole scales of *S. pellucidopunctata* are of slightly different shape than those of *S. ichthiosma*, being lanceolate and falcate rather than ovate and symmetrical. In Ecuador, *S. pellucidopunctata* occurs only on the eastern side of the Andes, whereas *S. ichthiosma* occurs only on the western side.

←

FIGURE 25. *Stigmatopteris pellucidopunctata*.—a. Proscales or microscales (uniseriate) and multiseriate scales from the abaxial surface of the lamina.—b. Leaf.—c. Basal portion of medial pinna.—d. Rachis and costae with linear-lanceolate scales.—e. Petiole scales. a, b, d, e, *Moran 3624*, MO. c, *van der Werff & Gudiño 11170*, MO.

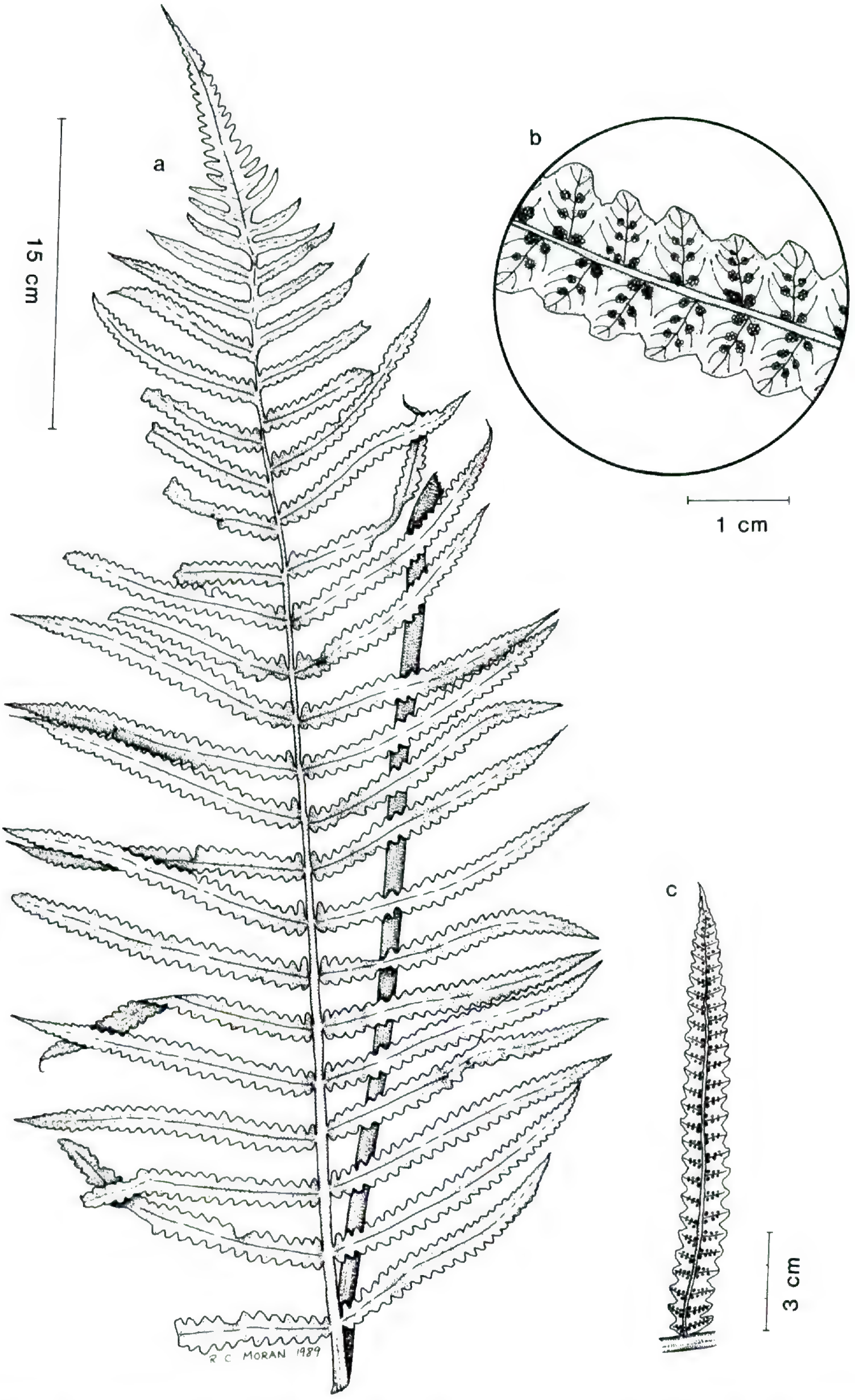


FIGURE 26. *Stigmatopteris prionites*.—a. Leaf (*Blanchet 2483*, BM).—b. Venation and sori (*Martius 305*, B).—c. Fertile pinna (*Martius 305*, B).

MAP 10. Distribution of *Stigmatopteris rotundata* (dots) and *S. prionites* (diamonds).

19. Stigmatopteris prionites (Kunze) C. Chr., Bot. Tiddskr. 29: 298. 1909. *Dryopteris prionites* (Kunze) C. Chr., Index Filic. 286. 1905. *Polypodium prionites* Kunze, Flora Beibl. 1: 29. 1839. TYPE: Brazil, from three states, see discussion below: *Martius 305* (lectotype, here designated, B; isolectotypes, BM, BR not seen, G, K, L, MO, NY; photo, BM ex BR). Figure 26. Map 10.

Stigmatopteris prionites var. *denticulata* (Fée) C. Chr., Bot. Tidsskr. 29: 299. 1909. *Phegopteris denticulata* Fée, Crypt. Vasc. Brésil 1: 100, t. 32, fig. 2. 1869. TYPE: Brazil. Rio de Janeiro: fazenda de Santa Anna, *Glaziou 2400* pro parte (holotype, P; isotype, P).

Rhizome short-creeping; leaves to 1.5 m; petiole ca. equaling the lamina, stramineous to brown, scaly at the base, the scales 4–8 × 1–2 mm, brown, thin, lanceolate; lamina 1-pinnate-pinnatifid, lanceolate, lacking buds, only a few distalmost pinnae with short-decurrent bases; pinnae 11–20 × 1.1–2.3 cm, cut ¼–½ to the costa, pairs 19–26, the base sessile or nearly so; segments entire to denticulate at the apex, separated by broad, U-shaped sinuses; rachis and costae stramineous,

sparsely scaly, the scales ovate to lanceolate; veins free, not forked, 3–5 per lobe; sori inframedial; indusial scale absent.

Additional specimens examined. BRAZIL. BAHIA: no locality, *Luschnath 120* (B), 1836, *Blanchet 2483* (BM, G, P). ESPÍRITO SANTO: Jatiboca, *Brade 18405* (G, GH, MO, NY, P). MINAS GERAIS: Juiz de Fora, Rio do Peixe, *Krueger 17107* (UC); Viçosa, Corrigo Riberro, Agricultural College, 675 m, *Mexia 4893-a* (UC); Distrito Rio Branco, Retiro de Antonio Avelino, 740 m, *Mexia 5492* (F, GH, K, NY, P, UC, US, Z). STATE UNKNOWN: Mt. Parahyba, 1886, *Goldi s.n.* (G); Brasilia, *Riedel s.n.* (US); no locality, *Glocker 32* (BM, US).

Stigmatopteris prionites is endemic to southeastern Brazil (Map 10) where it grows in wet forests from 500 to 740 m. It can be distinguished from all other *Stigmatopteris* in Brazil by the combination of narrow (1.1–2.2 cm) pinnae cut up to halfway to the costa, broad, obtuse lobes with wide sinuses, few (3–5) veins per lobe, and inframedial sori. The fertile pinnae are slightly narrower than those of the sterile.

Variety *denticulata* differs by having more deeply lobed pinnae with the lobes denticulate at the apex. Because this character intergrades with plants having entire lobes, the variety is here placed in synonymy.

The type collection has a varied provenance. Although none of the specimens have a more specific locality than "Brazil," the original description by Kunze states that *Martius 305* comes from the provinces of Bahia (Porto Seguro), Espírito Santo, and Rio de Janeiro. Therefore, I chose the sheet at Berlin (B) as the lectotype.

20. Stigmatopteris pterorhachis R. C. Moran, sp. nov. TYPE: Colombia. Magdalena: Santa Marta, Sierra del Libano, 1,800 m, *H. H. Smith 1045* (holotype, MO; isotypes, BM, DUKE, F, GH, MICH, NY, P, UC, US). Map 8.

Folia 1-pinnata, pinnis 4–7 utroque costae latere, gemmis absentibus; rhachis costaeque abaxialiter glabrae; venae irregulariter anastomasantes.

Rhizome short-creeping, the internodes 0.5–2 cm, scaly at the apex, the scales 1–3 mm, ovate to lanceolate, opaque, brown, rigid, entire; leaves 50–110 cm; petiole ca. equaling the lamina, dull brown or tan on both surfaces, lacking hairs, scaly, the scales 4–9 mm, translucent, spreading, brownish, lanceolate; lamina 1-pinnate, oblong-deltate, bulblets lacking; free pinna pairs (3–)4–7; basal pinnae usually somewhat reduced, widest near the middle, stalked, the stalk 2–4 mm; medial pinnae (10–)15–20 × 2.5–3.5 cm, widest at or near the base, the margins entire to deeply crenate; distal pinnae with long-decurrent bases; rachis and costae tan, light brown, or stramineous, lacking hairs, scaly, the scales to 1 mm, 1–2 cells wide, filamentous, usually with a long central filament and several shorter ones branched from the point of attachment; veins part free and part anastomosing, the areoles with 1 or 2 curved, irregular or forked excurrent veinlets; sori discrete, indusial scale absent.

Additional specimens examined. VENEZUELA. LARA: Dtto. Morán, 1,500 m, *Rivero et al. 1602* (PORT, UC); Dtto. Menez, between Cubiro and Escalera, 10–15 km SW of Cubiro, 1,600–2,000 m, *Steyermark et al. 110227* (F). PORTUGUESA: Dtto. Sucre, Los Paramitos, a 20 km por aire al SO de Biscucuy, 1,000–1,500 m, *Ortega et al. 1822* (MO, PORT); Dtto. Guanare, ESE of Paraíso de Chabasquén, along road to Cordoba, ca. 27 minutes from Chabasquén, 1,500 m, *A. R. Smith 1031* (AAU, CR, MO, PORT, UC, Z). COLOMBIA. MAGDALENA: Sierra Nevada, Río Macha, *Schlim 856* (K, P); Sierra Nevada de Santa Marta, finca Los Arroyitos, 1,600–1,700 m, *Kirkbride 2377* (NY, UC). NORTE DE SANTANDER: Ocaña, *Schlim 596* (BM, G, K).

Stigmatopteris pterorhachis occurs in northwestern Venezuela and northern Colombia (Map 8) where it grows primarily in cloud forests from 1,000 to 1,800 m. It greatly resembles *S. heterophlebia*, but differs by the absence of capitate glandular hairs on the axes, the presence of 1- or 2-cells-wide, filamentous, basally branched scales on the costae, and the greater number of pinna pairs. These characters correlate on all specimens except *Rivero et al. 1602*, which is moderately to sparsely glandular on the abaxial surface of the rachis, but lacks glands on that surface of the costae (unlike *S. heterophlebia*). The specimen is typical of *S. pterorhachis* in the other two characters, which separate it from *S. heterophlebia*.

The name *S. alloëoptera* (Kunze) C. Chr. has been previously misapplied to this species and to *S. heterophlebia* (see section on names of uncertain application).

21. Stigmatopteris rotundata (Willd.) C. Chr., Bot. Tidsskr. 29: 297. 1909. *Aspidium rotundatum* Willd., Sp. Pl. ed. 4, 5: 247. 1810. *Dryopteris rotundata* (Willd.) C. Chr., Index Filic. 289. 1905. TYPE: Plumier, Traité Foug. Amér. 29, t. 38. 1705, illustrating a plant from Martinique. Figure 27. Map 10.

Polypodium flavopunctatum Kaulf., Enum. Filic. 108. 1824. *Phegopteris flavopunctata* (Kaulf.) Fée, Mém. Foug. 11: 51. 1866. SYNTYPES: Martinique, *Sieber 350* (B, MO; photos, BM, F, G, GH, MO, NY, P, UC ex L); Martinique and Montserrat, *Ryan s.n.* (P-herb. Vahl).

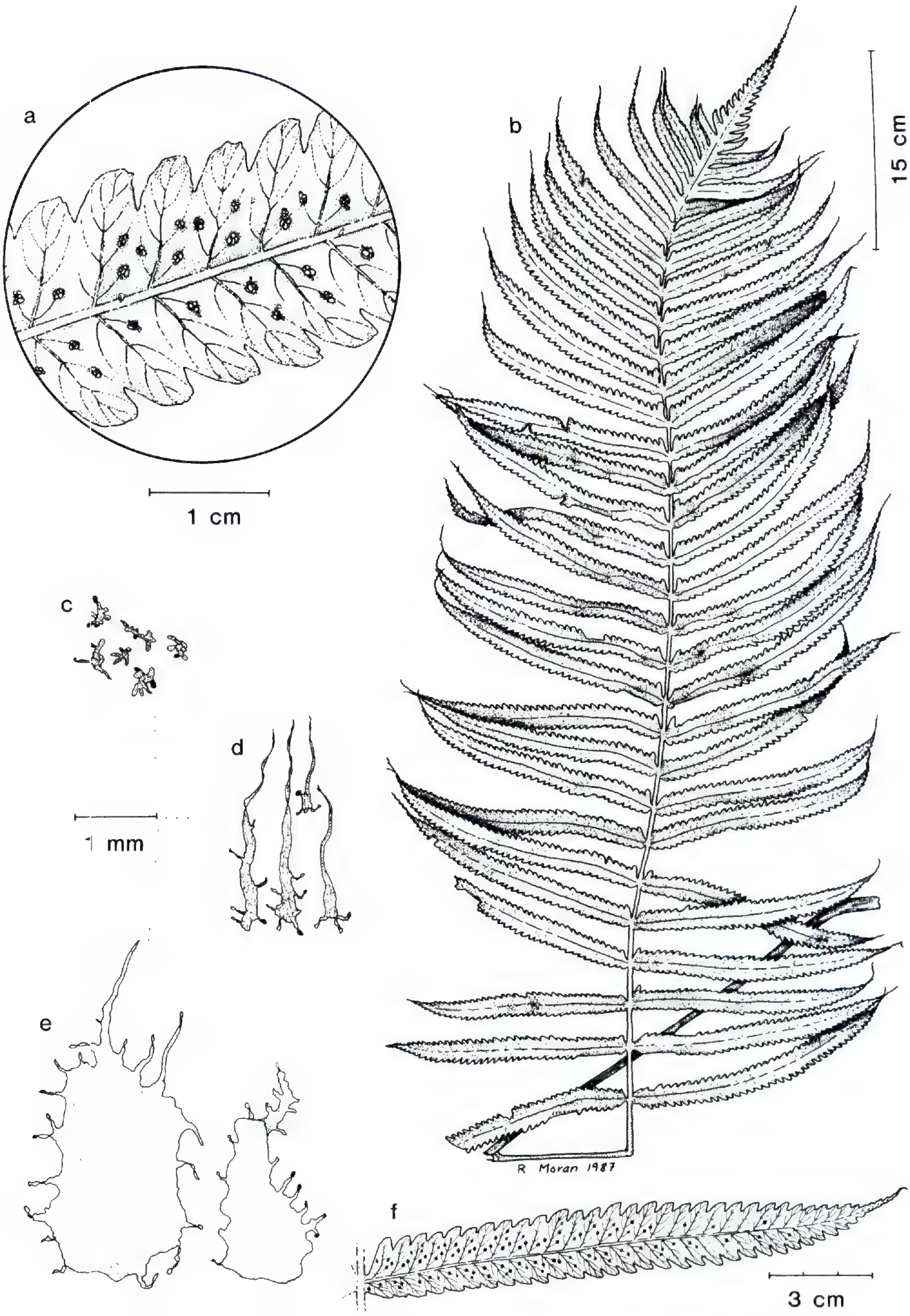


FIGURE 27. *Stigmatopteris rotundata*.—a. Venation and sori (*Morton 6184*, US).—b. Leaf (*Morton 6184*, US).—c. Costal scales (*Alston 494*, NY).—d. Costal scales (*collector unknown*, K-H1058/87).—e. Costal scales (*Duss 4074*, NY).—f. Fertile pinna (*collector unknown*, K-H1058/87).

Stigmatopteris rotundata var. *trinidadensis* C. Chr., Bot. Tidsskr. 29: 297. 1909. SYNTYPES: Trinidad. *Fendler 98* (B, BM, GH, K, MO, UC, US); Cabueres de Sarrapo, 11 Nov. 1863, *Hart 3707* (US, NY), *6259* (US) [these two numbers equal the Botanic Garden Herbarium of Trinidad nos. *337* and *1236*, respectively].

Nephrodium imrayanum Hook., Sp. Fil. 4: 86, t. 242.

1862. *Aspidium imrayanum* (Hook.) Fée, Mém. Foug. 11: 79. 1866. *Dryopteris imrayana* (Hook.) Domin, Rozpr. Král. Ceské Společn. Nauk,-Tř. Mat.-Přír. N.R., 21: 191. 1929. TYPE: Dominica. *Imray 17* (holotype, K; isotype, BM; photos, GH, US ex BM).

Rhizome short-creeping, the scales 2–4 mm, brown, entire, narrowly lanceolate; leaves to 2 m; petiole ½ to equaling the lamina, brown to tan, the scales all of one type, 5–12 × 1–2 mm, lanceolate, translucent, never blackish or thickened, entire, brown; lamina 1-pinnate-pinnatifid, oblong to oblong-lanceolate, lacking bulbils; pinnae 11–26 × 1.5–2.5(–3) cm, 18–32 pairs, linear or rarely narrowly lanceolate, crenate or cut less than ⅓(–½) to the costa; upper pinnae adnate to the rachis and confluent only in the distal ¼–⅛ of the lamina, the lower pinnae subsessile or stalked, the stalk to 8 mm; rachis and costae scaly, the scales ovate to lanceolate, filiform, or roundish to ovate and irregularly lobed; veins free, 3–4 per segment; sori lacking an indusiumlike scale, inframedial to supramedial, those on the basal veinlets often at the apex of the vein.

Additional specimens examined. GUADELOUPE. Morne du Calababbaye, *Belanger 821* (G); no locality, *Duss 80* (US); Bon du Marne de la Madeleine, Trois Rivières, *Duss 729* (P); Bois de la Calebasse, 450–900 m, *Duss 1561* (NY, P), Bois de la cascade de Vanchelet, 330–960 m, *Duss 4074* (NY, US); Forêt du Nez bassé, 1,000 m, *Le Gallos 2965* (P), *3100* (P); *L'herminier 115* (B, G, GH); no locality, *Marie 516* (F, G, P); Basse Terre, above Matouba, *Proctor 20345* (GH); Ravine Roche, *Questel 2905* (US); Gran Etang, 350 m, *Stehlé 1104* (US); ravine Malanga, 680 m, *Stehlé 1463* (US); Bains Jaunes, 1,050 m, *Stehlé 1887* (US). DOMINICA. Lagunem Roseau, *Eggers 905* [Toepffer no. 668] (B, G, P); Sylvania estate, 488 m, *Hodge 103* (GH, MO, NY, UC, US); Lisdara, *Hodge 104* (GH, US); Lisdara, 470 m, *Hodge 2377* (GH, NY, US); 1 mi. E of Laudat, ca. 665 m, *Hodge & Hodge 1972* (GH); no locality, *Imray 39* (B); St. Paul Parish, 0.5 mi. S of Pont Cassé, *Lellinger 362* (MICH, US); St. Paul Parish, *Lellinger 367* (DUKE, GH, US); St. Joseph Parish, S of Tiperie, N side of Morne Couronne, *Lellinger 507* (US); Mt. Diablotin, *Lloyd 902* (NY, US); St. John, Morne Diablotin, *Webster 13329* (DUKE, US); St. Joseph, ridge S toward McFarlin, *Webster 13566* (US), *13558* (MO, UC, US); above Bellevue along trail to Grand Bay, *Wilbur 7882* (DUKE). MARTINIQUE. No locality, *Belanger 821* (BM, K); Bois du Lorrain, *Duss 1561* (US); no locality, *Hahn 37* (B, BM, P); St. Denis, *Stehlé 3303* (US); Colson, 560 m, *Stehlé 4807* (US); Rivière Dumanée, 600 m, *Stehlé 4883* (UC, US); Bois de la Pirogue, Lorrain, 280 m, *Stehlé 6725* (US); Morne Rouge, 500 m, *Stehlé 7238* (US); vallée du Lorrain, 650 m, *Stehlé 8436* (MICH, US). ST. LUCIA. Mt. Gimie, *Box 1966* (BM). ST. VINCENT. No locality, *Checkley 7* (B); Charlotte Parish, Montreal, *Cooley 8325* (GH); no locality, *Eggers 6869* (F, US); along Chateaubelair River, 300–400 m, *Morton 5373* (GH, US); upper valley of Richmond River, 330–540 m, *Morton 6184* (US); no locality, *H. H. Smith & G. W. Smith 659* (B, BM, CM, GH). GRENADA. No locality, *Eggers 6164* (F, UC, US); St. Mark Parish, NW slope of Mt. St. Catherine, *Proctor 17244* (MICH, US); no locality, Oct.–May 1890–91, *Sherring s.n.* (BM, K, US). TRINIDAD. Mount Tocuche, *Britton et al. 1361* (F, NY, US); Morne Bleu, *Britton et al. 2250* (GH, NY, US); Maracas, *Broadway 5355* (BM, F, G, MO, NY, Z); Maracas Road to the bay, N via Santa Cruz, *Broadway 6123* (BM, MO); *Fendler 98* (B, BM, G, GH, K, MO, NY, UC, US); Morne Bleu, road near summit, *Johnston 303* (BM); Morne Bleu, Arima–Blanchisseuse road, *McCallum 104* (BM); Asa Wright Nature Centre, 7 mi. N of Arima, *Mickel 9412* (NY, UC); no locality, *Prestoe 214* (MO). FRENCH GUIANA. Montagne de l'Inini, zone centrale, 750 m, *Cremers 9113* (UC), *9140* (UC); Mt. Galbao, secteur Est, 3°36′N, 53°17′W, 600 m, *de Granville 8873* (UC); Montis Diabolis, in 1847, *Leprieur 270* (P). GUYANA. Ereugfaru, Maiewac River, along the Santa María trail, *Alston 494* (K, NY); Potaro River, 1899, *Jenman s.n.* (NY). VENEZUELA. BOLÍVAR: región de Urimán, 760 m, *Bernardi 938* (PORT); Uei-Tepui, between Luepa and Cerro Venamo, 1,100–1,300 m, *Steyermark & Nilsson 314* (NY, VEN). SUCRE: península de Paria, W de Cerro Humo, 700–750 m, *Steyermark & Rabe 96115* (NY, VEN).

Stigmatopteris rotundata, the type of the genus, occurs from 280 to 1,300 m in the Lesser Antilles, Guianas, and eastern Venezuela. Proctor (1977) listed this species from Montserrat and Kramer (1978) listed it from Suriname (*Versteeg 315*), but I have not seen a specimen from those countries.

The scales in *S. rotundata* are extremely variable. Most plants from the Lesser Antilles have filiform to lanceolate scales (Fig. 27d), but plants from Guadeloupe and (often) Dominica have 2–4-mm-long, broadly ovate, flaccid scales (Fig. 27e). Plants from South America have scales that are less than 1 mm long, roundish to ovate, and irregularly lobed (Fig. 27c). Because no other characteristics other than geography correlate with scale type, I feel it is best only to mention this variation rather than formally name it.

22. Stigmatopteris sordida (Maxon) C. Chr., Index Filic. Suppl. 3: 175. 1934. *Dryopteris sordida* Maxon, Contr. U.S. Natl. Herb. 24: 60. 1922. TYPE: Guatemala. Alta Verapaz: near Cubilquitz, 350 m, *von Türckheim 1432* (holotype, US; isotype, US). Figure 28. Map 11.

Stigmatopteris litoralis Rosenstock, Repert. Spec. Nov. Regni Veg. 22: 12. 1925. TYPE: Costa Rica. Limón: Finca Gebr. Hundrisser, *Brade & Brade 353* (holotype, S? not seen).

Rhizome short, ascending; leaves to 1.3 m; petioles ½ to about equaling the lamina, stramineous, tan or brown, the scales 3–10 × 1–2 mm, ovate

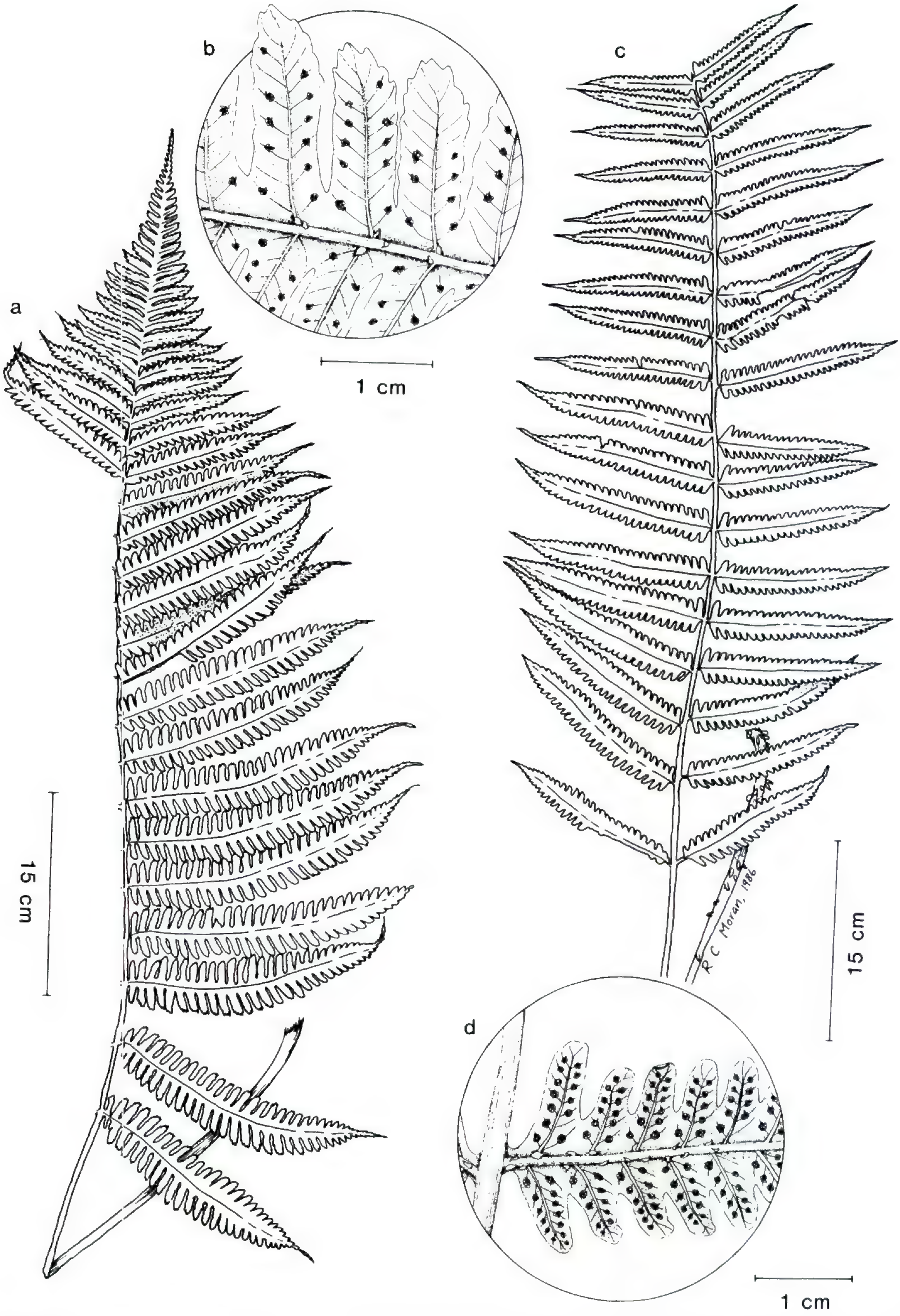
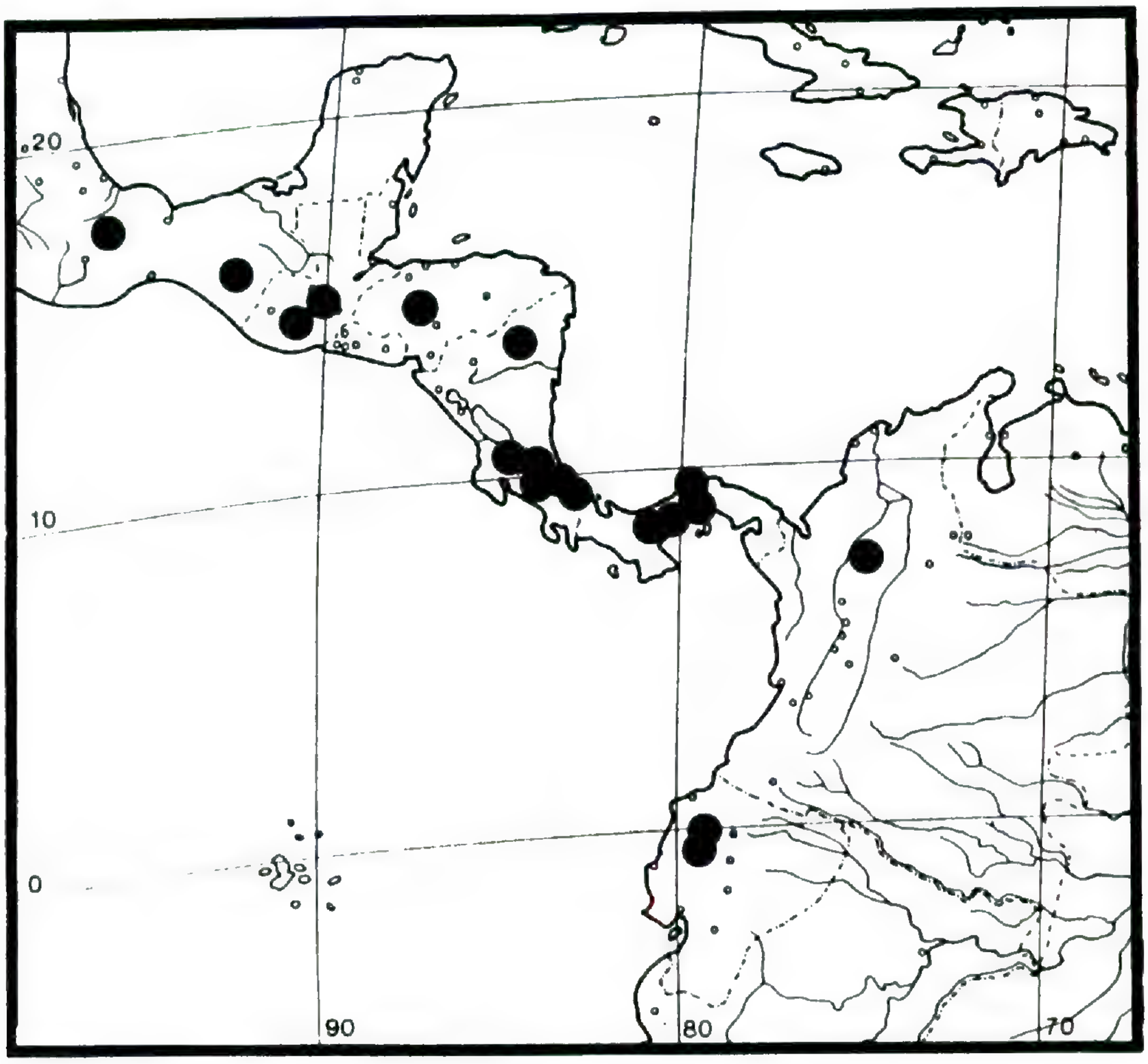


FIGURE 28. *Stigmatopteris sordida.*—a. Leaf.—b. Venation and sori.—c. Leaf.—d. Venation and sori. a, b, *Moran 3607*, MO. c, d, *Moran 3115*, MO.



MAP 11. Distribution of *Stigmatopteris sordida*.

to lanceolate, or lanceolate with an attenuate apex, entire, dark brown or rarely (in Colombia) yellow-brown; lamina 1-pinnate-pinnatifid, ovate, lanceolate, or narrowly long-triangular, buds lacking, only the distalmost pinnae with short-decurrent bases; pinnae 15–28 × 2–4 cm, usually cut between ½–¾ of the way to the costa or sometimes more in the enlarged basal pinnae, pairs 16–25, the basal ones stalked, those above gradually becoming sessile then adnate, the basal basiscopic lobe not overlapping the rachis (although sometimes adnate to it), the basal acroscopic lobe often prolonged; lobes rounded, entire or serrate at the apex; rachis and costae stramineous or the rachis brown, or sparsely scaly, the scales ovate to lanceolate; veins generally 7–10 per lobe, unbranched or rarely with a short acroscopic branch; sori medial, lacking an indusiumlike scale.

Additional specimens examined. MEXICO. CHIAPAS: Finca Mexiquito, *Purpus 6870* (BM, F, GH, MO, NY, UC, US); no locality, *Purpus 7256* (GH). OAXACA: Dtto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, trail E of Rte. 175 at Campamento Vista Hermosa toward Ladú, 500–850 m, *Mickel 6403* (NY, UC). GUATEMALA. SUCHITEPÉQUEZ: S slope of Volcán Atitlán, Finca Mocá, Guatalon, ca. 250 m, *Hatch & Wilson 346* (US). HONDURAS. COMAYAGUA: Aldea de "Varsovia," 24 km SE del lago de Yojoa, 600 m, *Claros 73* (MO). NICARAGUA. ZELAYA: Costado sur del Cerro La Pimienta y N del Cerro Hormiguero, a Orilla del Caño Hormiguero, 800–900 m, *Grijalva 290* (MO). COSTA RICA. ALAJUELA: near Río San Rafael, 2 km W of La Marina, Llanura de San Carlos, 550 m, *Molina R. et al. 17321* (CR, NY); 11 mi. NW of Zarcero, 850 m, *Croat 43598* (CR, MO); W of Marina, 500 m, *Burger & Stolze 5055* (CR, F, MO), *5057* (CR, F, GH, NY, US); between San Lorenzo and Los Angeles de San Ramón, above Río San Lorenzo, 620 m, *Burger & Antonio 11179* (CR, F); Río Chiquito, ca. 40 km on road to Upala, 800 m, *Gómez 18641* (MO, UC). CARTAGO: E of Turrialba, 900 m, *Lellinger & White 1428* (CR, MO, US). HEREDIA: Finca La Selva, Puerto Viejo de Sarapiquí, ca. 60–80 m, *Grayum 2641* (UC); Cerro Sardinal, ca. 2–2.5 km N of Chilamate de Sarapiquí (Finca La Martita), 80–160 m, *A. R. Smith et al. 1813* (UC); between Río Peje and Río Guácimo, 230 m, *Grayum & Jacobs 3598* (MO); Finca La Selva, OTS Field Station, 100 m, *Hammel 11495* (MO), *12382* (CR, MO). LIMÓN: Dist. Talamanca–Canton, ca. 3 km SW of Suretka, near RECOPE test drill site, 70 m, *Moran 3115* (CR, F, MO); Talamanca, Bri-Bri, *Ocampo S. 1771* (CR). SAN JOSÉ: Parque Nacional Braulio Carrillo, Fila Carrillo, 600–700 m, *Chacón 319* (AAU, MO, UC); 25 km S of Villa Mills on the way to San Isidro on the Interamerican Highway, ca. 1,450 m, *Mickel 3283* (NY, US). PANAMA. CANAL ZONE: Barro Colorado Island, *Kenoyer 34* (US); Barro Colorado Island, *Knight s.n.* (US); Parque Nacional Soberanía, camino del Oleoducto, *Vásquez 188* (MO, US). COCLÉ: road to Coclesito, logging camp, 12 mi. from Llano Grande, *Churchill et al. 4089* (MO); El Valle de Antón, 1,000 m, *Alston 8744* (BM). COLOMBIA. ANTIOQUIA: Municipio de Zaragoza, Corregimiento de Provedencia, 500–

650 m, *Soejarto & Villa 2685* (COL, GH). ECUADOR. LOS RÍOS: Río Palenque Science Center, 56 km N of Quevedo, *Moran 3607* (MO, QCA, QCNE), *Grayum & Zamora 9376* (MO). PICHINCHA: NE of Vicente Maldonado, Reserva de ENDESA, 600 m, *Laegaard 51610* (AAU).

Stigmatopteris sordida occurs from southern Mexico to Ecuador (Map 11) from 70 to 1,450 m. Maxon (1922), in his original description of this species, stated that the ultimate segments are never serrate, but the type has some serrations on the sterile segments. Specimens that have been collected since 1922, from Central and South America, show that the segment margins vary from entire to serrate. The specific name is derived from the Latin word *sordidus*, meaning dirty-looking, dingy, or soiled. I am uncertain what this refers to.

Although I did not see the type, *S. litoralis* is put here in synonymy because of the original description and because the type was collected from the Atlantic lowlands of Costa Rica where *S. sordida* is common. *Stigmatopteris longicaudata* also grows in the Atlantic lowlands but can be excluded from consideration because the original description of *S. litoralis* stated that the pinnae are cut ¾ to the costa and only the distalmost pinnae are short decurrent—characteristics unlike *S. longicaudata*.

23. Stigmatopteris tyucana (Raddi) C. Chr., Bot. Tidsskr. 29: 298. 1909. *Polypodium tyucanum* Raddi, Opusc. Sci. 3: 288. 1819. *Dryopteris tijuccana* (Raddi) C. Chr., Index Filic. 298. 1905. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, Gavia, Mt. Tijùca, *Raddi s.n.* (holotype, FI or PI not seen). Figure 29.

Aspidium brachyneuron Fée, Crypt. Vasc. Brésil 1: 133. 1869. TYPE: Brazil. Bahia: *Blanchet s.n.* (P? not seen).

Phegopteris tenuis Fée, Crypt. Vasc. Brésil 1: 99, t. 30, fig. 1. 1869. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Glaziou 964* (holotype, P).

Rhizome short-creeping; leaves to 1.2 mm; petiole ca. equaling the lamina, stramineous to brown, scaly at the base, the scales 5–12 × 1–2 mm, brown, thin, lanceolate; lamina 1-pinnate-pinnatifid, lanceolate, lacking bulblets, only a few distalmost pinnae with short-decurrent bases; pinnae 12–20 × 2.5–4 cm, 12–15 pairs, cut ⅓–½ to the costa, the base sessile or nearly so, the basal pinnae short-stalked; segments entire; rachis and costae stramineous, sparsely scaly, the scales ovate to lanceolate; veins free, not forked, 4–7 per lobe; sori medial to supramedial; indusial scale absent.

Additional specimens examined. BRAZIL. RIO DE JANEIRO: Colonia Leopoldiana, 1836, *Blanchet 2483* (BM); Terezópolis, Ilindinho, 450 m, *Brade 9972* (GH, UC); Teresópolis, *Brade 9977* (NY); Rio de Janeiro, *Gaudichaud s.n.* (G); Petrópolis, Cascatinha, *Glaziou 7245* (B, K, P, US); no locality, *Martius s.n.* (B). SÃO PAULO: Alto da Serra, *Brade 5892* (NY, UC); Serra do Mar, 300 m, *Wacket 50* (NY, UC); Alto da Serra, Parque Cajurú da estacion biológica, *Wacket 21149* (BM, NY, UC), *Luederwaldt 21149* (GH, UC). STATE UNKNOWN: near Rio de Janeiro and Bahia, *Webb s.n.* (MICH); no locality, *Riedel s.n.* (B, GH).

Stigmatopteris tyucana is endemic to southeastern Brazil where it grows in wet forests from 300 to 400 m. The specific epithet is usually spelled *tijuccana*. I prefer to spell it *tyucana* because that was Raddi's original spelling, and the *Code* (Greuter et al., 1988) recommends the use of the author's original spelling (when not in error).

Although I have not seen the type, I am confident from Raddi's excellent illustration (1825, t. 37) and description that the name is here applied correctly.

24. Stigmatopteris ulei (Christ) Sehnem, Fl. Illust. Catar. 1ASPI: 100, est. 25, fig. 2. 1979. *Phegopteris ulei* Christ, Bull. Herb. Boissier sér. 2, 2: 634. 1902. *Dryopteris ulei* (Christ) C. Chr., Index Filic. 299. 1905. TYPE: Brazil. Santa Catarina: município de São Francisco do Sul, Serra de Laranjeira, *Ule 70* pro parte (holotype, P? not seen).

Lamina 1-pinnate-pinnatifid, apparently lacking buds; pinnae cut ca. ⅔ to the costa, the distal ones (presumably) lacking a basal basiscopic lobe adnate to the rachis; the lobes nearly entire, separated by broad, U-shaped sinuses; veins free, 5–8(–10) per lobe; sori inframedial.

I have the type number from P of *Ule 70*, but the locality given on the sheet (im schattigen Urwald der Peninsula da Gloria, Feb. 1884) is different from that given in Christ's original description. The specimen is *Stigmatopteris caudata*. The only specimen that I have seen of *S. ulei* is the photograph of a medial pinna in Sehnem (1979). Because I have not seen a herbarium specimen, the above description is incomplete. *Stigmatopteris ulei* is included in the key and the species descriptions, rather than the uncertain taxa section, to call attention to this poorly known species and because, on the basis of Sehnem's photograph, it appears distinct.

Christensen (1913) thought that this species was probably a form of *S. prionites*, but *S. ulei* is intermediate in cutting—perhaps a hybrid?—be-

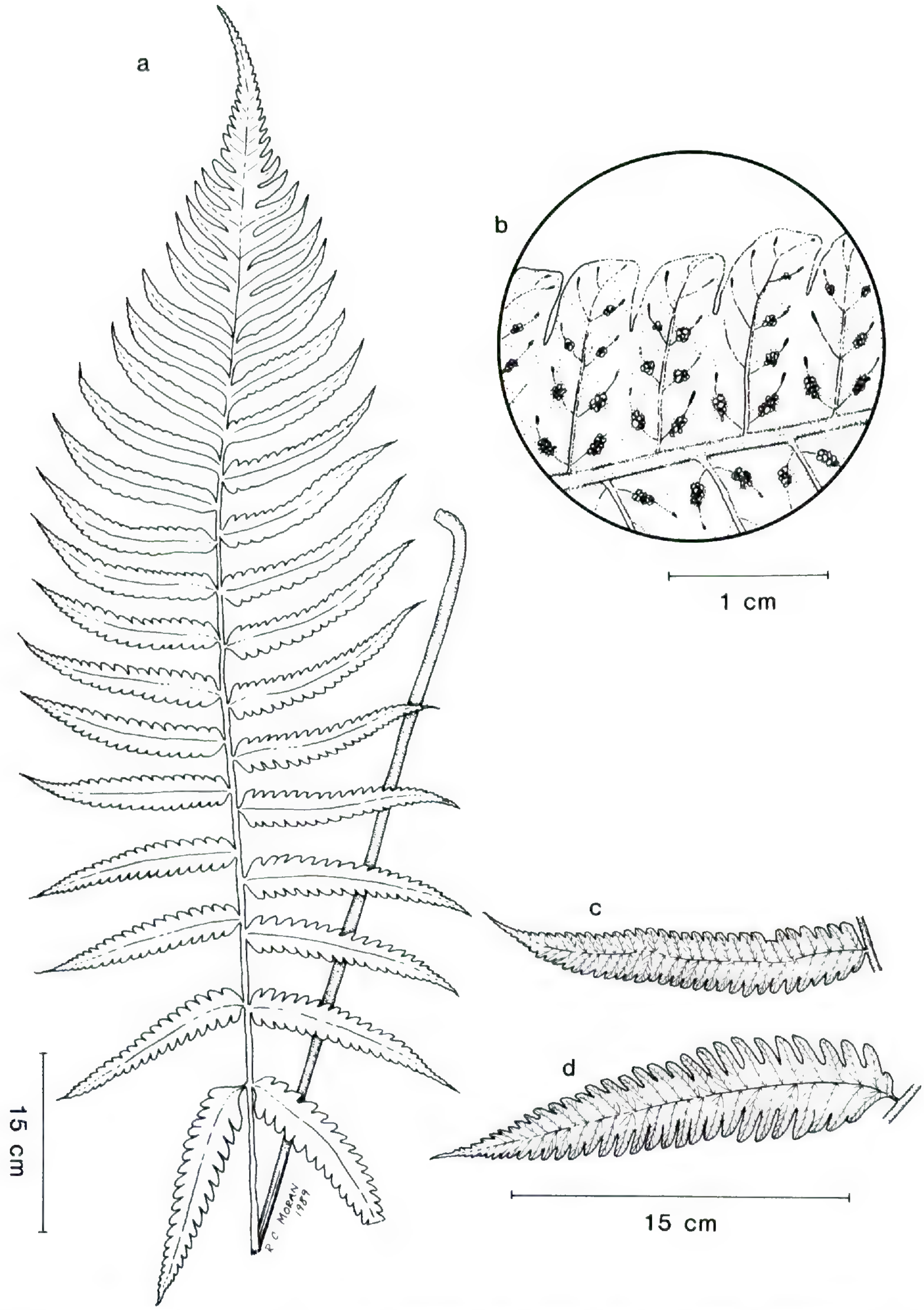


FIGURE 29. *Stigmatopteris tyucana*.—a. Leaf (redrawn from Raddi, 1825, t. 37; scale approximate).—b. Veins and sori.—c. Medial pinna (*Brade 9977*, NY).—d. Basal pinna (*Brade 9977*, NY).

tween *S. caudata* and *S. brevinervis*. The intermediate cutting is evident in Sehnem's (1979) photograph, which has *S. ulei* placed between *S. caudata* and *S. brevinervis*. Sehnem (1979) cited the following specimen for *S. ulei*: Brazil. Paraná: Paranagua, Morro de Tabaquara, terrícola na mata pluvial de encosta de morro, 50–100 m, *Hatschbach & Imaguire 16361*. Obviously, it is difficult to assess whether *S. ulei* represents a hybrid without having specimens for study.

EXCLUDED TAXA

Dryopteris subg. *Stigmatopteris*, group *Peltochlaena* Fée ex C. Chr., Kongel. Danske Vidensk. Selsk.

Skr., Naturvidensk. Afd. ser. 7, 10: 74. 1913. = *Cyclodium* C. Presl (fide Smith, 1986).

Stigmatopteris clypeata (Maxon & C. Morton) Lellinger, Proc. Biol. Soc. Wash. 89: 730. 1977. = *Thelypteris clypeata* (Maxon & C. Morton) Kramer (fide Kramer, Acta Bot. Neerl. 18: 141. 1969).

Stigmatopteris guianensis (Klotzsch) C. Chr., Index Filic. Suppl. 3: 173. 1934. = *Cyclodium guianense* (Klotzsch) A. R. Smith (fide Smith, 1986).

Stigmatopteris meniscioides (Willd.) Kramer in Kramer & van Donselaar, Koninkl. Nederl. Akad. Wetensch. Proc. 71: 521. 1968. = *Cyclodium meniscioides* (C. Morton) A. R. Smith (fide Smith, 1986).

Stigmatopteris paludosa (C. Morton) R. Tryon & A. Tryon, Rhodora 83: 136. 1981. = *Cyclodium meniscioides* var. *paludosum* (C. Morton) A. R. Smith (fide Smith, 1986).

Stigmatopteris sancti-gabrieli (Hook.) C. Chr., Index Filic. Suppl. 3: 175. 1934. = *Cylcodium guianense* (Klotzsch) A. R. Smith (fide Smith, 1986).

Stigmatopteris varians (Fée) Alston, Kew Bull. 1932: 309. 1932. = *Cyclodium varians* (Fée) A. R. Smith (fide Smith, 1986).

Names of Uncertain Application

Stigmatopteris alloëoptera (Kunze) C. Chr., Bot. Tidsskr. 29: 300. 1909. *Polypodium alloëopterum* Kunze, Linnaea 25: 748. 1835. TYPE: Venezuela. Distrito Federal: near Galipán, 1,200–1,500 m, Sep., *Wagner 460* (LZ—destroyed).

This name does not represent *S. heterophlebia* or *S. pterorhachis* (previously treated as one), to which it was applied by all previous pteridologists. There are three reasons why this former application cannot stand. First, Kunze described the pinnae of *Polypodium alloëopterum* as deeply incised-crenate, yet the pinnae of the former two species are only entire to deeply crenate. Second, Kunze likened the leaf of *S. alloëoptera* to that shown in Raddi's plate of *S. tyucana*; yet *S. tyucana* lacks the broad, decurrent, pinna bases that are distinctive for *S. heterophlebia* and *S. alloëoptera*. In addition, Raddi's plate clearly shows a leaf with deeply lobed pinnae and free veins. Third, *S. heterophlebia* and *S. pterorhachis* have never been found in the coastal mountains around Caracas where the type was collected—this despite much collecting activity in that area.

The only species of *Stigmatopteris*—and a common one—which occurs around Caracas is *S. nephrodioides*. This species has deeply lobed pinnae, free veins, and is like the leaf pictured in Raddi's plate. I strongly suspect, but cannot prove, that *P. alloëoptera* applies to *S. nephrodioides*, the later name. I do not, however, want to replace the well-known name *S. nephrodioides* with *S. alloëoptera* because I have not seen the type of *S. alloëoptera* and because *S. nephrodioides* has been widely used.

Phegopteris perforata Fée, Mém. Foug. 5: 248. 1852. TYPE: Country and collector unknown (P—herb. Mougeot).

Christensen (1920), who apparently saw the type, said that this name applied to a species of *Stigmatopteris* and was "badly described on an imperfect specimen of unknown origin. The name ought to pass into oblivion." Among Fée's specimens received from Paris (P), I did not see any specimens with this name.

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Index to Collectors' Numbers

This monograph is based on the specimens cited below, which consist of about 1,500 herbarium sheets from approximately 530 collections in 25 herbaria (see acknowledgments for the list of herbaria). Types are in boldface. The abbreviations in parentheses refer to the following species of *Stigmatopteris*, which are arranged alphabetically in the taxonomic treatment.

brev = *brevinervis*; bulb = *bulbifera*; caud = *caudata*; chim = *chimalapensis*; cont = *contracta*; gemm = *gemmipara*; hemip = *hemiptera*; het = *heterocarpa*; hp = *heterophlebia*; ic = *ichthiosma*; jam = *jamaicensis*; kil = *killipiana*; lech = *lechleri*; long = *longicaudata*; mi = *michaelis*; ne = *nephrodioides*; opaca = *opaca*; pp = *pellucidopunctata*; pri = *prionites*; pter = *pterorhachis*; ro = *rotundata*; sord = *sordida*; tyu = *tyucana*.

Aguilar 861 (long); 865 (long); 927 (pp). Allard 22558 (long). Alston 494 (ro); 8744 (sord); 8745 (hp); 8803 (kil); 8848 (kil). Alston & Lutz 289 (caud). Antonio 2050 (hp). Armond 557 (kil). Aymard et al. 3747 (lech).

Baker 5934 (hp). Barringer & Gómez-Laurito 2583 (hp). Barrington 410 (long). Beck 1625 (long); 8500 (pp). Belanger 821 (ro). Bernardi 938 (ro). Blanchet 2483 (tyu, pri). Bohs et al. 1704 (long). Box 1966 (ro). Brade 5892 (tyu); **8231** (het); **8250** (brev); 8340 (brev); 8343 (brev); 8473 (het); 8474 (het); 8476 (het); 8478 (caud); 8510 (het); 9972 (tyu); 9977 (tyu); 18228 (caud); 18405 (pri). Brade & Brade **353** (sord); **497** (long). Brant et al. 1679 (pp). Breedlove 35028 (long); 35128 (long); 56494 (long). Breedlove & Smith 32672 (long). Britton et al. 1361 (ro); 2250 (ro); Broadway 5355 (ro); 6123 (ro). Buchtien 64 (long); 233 (long); 2166 (long). Burger & Antonio 11179 (sord). Burger & Liesner 6773 (long). Burger & Stolze 5055 (sord); 5057 (sord). Burger et al. 10735 (cont).

Calzada 5212 (long). Cardénas 1020 (long). Cazelet & Pennington 5276 (ic). Chacón 319 (sord); 852 (long); 1776 (hp). Chacón & Herrera 1624 (hp). Checkley 7 (ro). Chrysler 4777 (jam). Churchill 5255 (hp). Churchill et al. 4089 (sord); 4549 (hp); 5984 (long). Claros 73 (sord). Clausen 133 (caud). Clement 633 (hemip); 674 (hemip); 945 (hemip); 949 (hemip); 961 (hemip). Conant 792 (long). Cooley 8325 (ro). Cornman 914 (cont); 1091 (cont); 1180 (hp); 1210 (hp); 1284 (hp). Cremers 9113 (ro); 9140 (ro). Croat 22998 (long); 25818 (long); 27477 (hp); 27541 (long); 27736 (long); 36176 (long); 37492 (long); 43598 (sord); 48097 (long); 49916 (hp); 54475 (ne); 60576 (ne); 60765 (ne); 66559 (hp); 68108 (caud); 68154 (sord); 68882 (kil); 69108 (long); 69137 (hp); 70911 (bulb). Croat & Grayum 60043 (hp); 60177 (long); 60215 (long); 60216 (hp); 60217 (hp). Croat & Liesner 1010 (hp). Crosby et al. 521 (jam). Cuatrecasas 15122 (long); 15240 (long); 17336 (hp).

de Granville 1291 (long); 1434 (long); 8873 (ro). de la Sota 5238 (cont). Dombrowski & Saito 1232 (caud). Dryer 366 (long); 396 (hp). Dusén 725a (brev); 2538 (caud); 10244 (het); 10341 (caud); 13727 (brev); 14115 (het); 14680 (het); 14687 (caud). Duss 80 (ro); 729 (ro); 1561 (ro); 4074 (ro).

Eggers 905 (ro); 6164 (ro); 6869 (ro). Ekman 5268 (gemm); 7424 (gemm); 10113 (gemm); 14356 (hemip). Elias 8 (pp). Evoy 44 (kil). Ewan 16775 (hp).

Fendler **98** (ro); 198 (ne). Finch 169 (long), Forero et al. 2309 (hp); 7407 (hp); 8793 (het). Foster P-84-91 (long). Foster & Wachter 7437 (pp). Foster et al. 10908 (long). Franco et al. 1148 (kil). Funck & Schlim 411 (ne).

Gardner 131 (caud). Glaziou **964** (tyu); 2396 (caud); **2400** (het, brev, pri); **2401** (het); 3333 (brev); 6414 (caud); 7245 (tyu). Glocker 32 (pri). Gómez 281 (cont); 987 (hp); 1133 (cont); 2182 (long); 2330 (cont); 3522 (hp); 18641 (sord); 18778 (long); 19288 (hp). Gómez & Wagner 6856 (long); 79027 (cont). Gómez et al. 19173 (hp); 20858 (hp). Gómez-Pompa et al. 5457 (long). González 14 (long). Grayum 2641 (sord); 4570 (cont); 5374 (cont); 6651 (hp); 6893 (long). Grayum & Jacobs 3598 (sord). Grayum & Schatz 3089 (long). Grayum & Sleeper 3683 (long); 3714 (cont). Grayum & Zamora 9375 (kil); 9376 (sord). Grayum et al. 3288 (hp); 5043 (hp); 5495 (kil); 7910 (long); 7922 (lech). Grijalva 290 (sord). Guzmán-Valdez 892 (long).

Haerchen 106 (het). Hagemann & Leist 2072 (bulb). Hahn 37 (ro); 352 (long). Hallberg 1724 (long). Hammel 2227 (hp); 4858 (kil); 11495 (sord); 12382 (sord). Hammel & de Nevers 13578 (hp). Hammel & Kress 13398 (mi). Hammel & Zuchowski 13880 (hp). Hammel et al. 14238 (long); 14827 (kil). Harling et al. 19737 (opaca). Harris 7277 (jam); 7419 (jam). Harrison **59** (hp). Hart 200 (jam); 337 (ro); **1236** (ro); **3707** (ro); **6259** (ro). Hatch & Wilson 346 (sord). Hatschbach 10748 (het); 22873 (caud); 24376 (het); 24739 (caud); 25939 (het); 41955 (het). Hatschbach & Scherer 26665 (caud). Haught 1931 (pp). Hazlett 3029 (long). Heinrichs 550 (bulb). Hellwig 491 (long); 492 (long); 494 (long). Hernández **1282** (chim). Herrera Ch. et al. 162 (hp); 316 (hp); 336 (cont); 2175 (sord); 2980 (lech). Hioran & Clement 6442 (hemip). Hodge 103 (ro); 104 (ro); 2377 (ro). Hodge & Hodge 1972 (ro). Holm-Nielsen & Jeppesen 811 (hp); 992 (opaca). Holm-Nielsen et al. 2906 (opaca); 24819 (ic). Hoover et al. 4304 (hp); 4325 (hp).

Imray 17 (ro); 39 (ro).

Jansson 740a (caud). Jenman 60 (jam). João & Rohr 392 (het). Johnston 303 (ro).

Kalbreyer **1807** (mi). Karsten **9** (ne). Kenoyer 34 (sord). Killip 2919 (kil); 5159 (cont); 5344 (long); 5387 (hp); 5444 (long); 12147 (kil). Killip & Smith 23906 (long); 28984 (hp). Kirkbride 2377 (pter). Krueger 17107 (pri). Kummrow & Hatschbach 2536 (het).

Laegaard 52431 (long); 51610 (sord); 51611 (hp); 51614 (opaca); 52224 (mi). Lancaster 836 (cont); 893 (hp). Lechler **2497** (lech). Le Gallos 2965 (ro). Lehmann 8951 (hp). Lellinger 362 (ro); 367 (ro); 507 (ro). Lellinger & de la Sota **194** (kil). Lellinger & White 1412 (hp); 1428 (sord); 1476 (hp). Leprieur 270 (ro). León, B. et al. 311 (pp). León, Fre. et al. 10311 (hemip); 10409 (hemip); 10486 (hemip); 11133 (hemip). L'Herminier 115 (ro). Liebmann **737** (long); **738** (long); **739** (long); **2694** (long). Linden 1683 (jam). Liesner & Holst 21882 (long). Liesner & Medina 13739 (ne). Liesner & Stannard 16909 (long). Lloyd 902 (ro). Luederwaldt 21149 (tyu); 21821 (caud). Luschnath 120 (pri).

MacDougal et al. 3811 (long). Madison et al. 3472 (lech). Maguire et al. 36864 (long). Marie 516 (ro). Martius **305** (pri). Maxon 790 (jam); 1071 (jam); **1738** (jam); 2388 (jam); 5647 (long); 8898 (jam); 8863 (jam); 9158 (jam); 9307 (jam). Maxon & Harvey 8075 (long). Maxon & Killip 7 (jam); 169 (jam); 716 (jam). McAlpin 1043 (long); 1313 (hp); 1326 (hp); 1396 (kil). McCallum 104 (ro). McDonough et al. 371 (mi). McPherson 6774 (hp); 8885 (long); 9730 (hp); 12035 (long); 12310E (long); 12677 (hp). Mendonca 1355 (caud). Mexia 4893-a (pri); 5492 (pri). Mickel 484 (long); 975 (long); 990 (long); 1523 (long); 2241 (cont); 2249 (cont); 2622 (hp); 2955 (hp); 3283 (sord); 3430 (cont); 3447 (hp); 5662 (long); 6369 (long); 6392 (long); 6403 (sord); 9412 (ro). Mickel & Pardue 6543 (long); 6727 (long). Molina R. et al. 17321 (sord). Moran 3165 (hp); 3166 (cont); 3187 (cont); 3188 (hp); 3206 (long); 3315 (sord); 3330 (cont); 3545 (ic); 3562 (kil); 3576 (opaca); 3582 (lech); 3607 (sord); 3611 (kil); 3613 (hp); 3624 (pp); 3696 (lech); 4048 (long); 4130 (hp); 5119 (lech); 5250 (ic). Morton 5373 (ro); 6184 (ro); 9569 (hemip). Mosén 2694 (caud). Moya 0011 (lech). Müller 1038 (brev).

Nee & Schatz 19868 (long). Nee et al. 26382 (long). Neill 1886 (hp); 3826 (hp). Nisman S. 98 (cont).

Ocampo S. 1029 (hp); 1771 (sord). Oliveira & Cordeiro 909 (het). Øllgaard et al. 35212 (pp); 35859 (opaca); **35866** (bulb); 39229 (hp); 57515 (long); 90435 (opaca). Ortega & González 369 (ne). Ortega et al. 1822 (pter).

Pabst 799 (het). Palacios 4030 (lech). Perkins 1161 (jam); 1613 (jam). Pittier 12172 (ne). Prestoe 214 (ro). Proctor 4257 (gemm); 17244 (ro); 20345 (ro); 32327 (hp); 38712 (opaca). Purpus 7256 (sord).

Questal 2905 (ro).

Ravins 961 (hemip). Regnell 254a (caud); 358 (caud). Reitz C205 (caud); C206 (brev); 227 (caud); 276 (brev); C919 (het); 1909 (caud); 3141 (het); 3542 (cuad). Reitz & Klein 3068 (het); 3077 (caud). Rivero et al. 1602 (pter). Rohr 352 (brev); 392 (het); 1006 (het); 1072 (caud). Rovirosa 822 (long).

Scamman 7667 (hp). Schenck 494 (het); 794 (pri). Schlim 596 (pter); 856 (pter); **1683** (= pp, but syntype of cont). Schmalz 106 (het); 191 (caud). Sehnem 808 (het); 3086 (het). Sieber **350** (ro). Skutch 145 (jam). Smith, A. R. 1031 (pter); 1692 (hp); 2121 (hp). Smith, A. R. et al. 1678 (long); 1813 (sord); 1862 (cont); 1876 (hp); 2194 (long); 2235 (hp); 2247 (cont). Smith, H. H. **1045** (pter). Smith, H. H. & G. W. Smith 659 (ro). Smith, L. B. 1391 (caud). Smith, L. B. & Reitz 6127 (het). Sodiro 48/1 (ic); **54/2** (opaca); **54/3** (opaca); **2615** (mi). Soejarto & Villa 2685 (sord). Solomon 18469 (long.) Spannagel 332 (het). Spruce 4012 (long); **4653** (opaca); **4719** (lech); **4720** (pp); 5714 (ic). Standley 37169 (hp); 37834 (cont). Standley & Torres R. 51061 (cont); 51069 (hp). Stehlé 1104 (ro); 1463 (ro); 1887 (ro); 3303 (ro); 4807 (ro); 4883 (ro); 6725 (ro); 7238 (ro); 8436 (ro). Steyermark 61403 (ne); 89747 (ne). Steyermark & Espinoza 111174 (ne); 111493 (ne). Steyermark & Nevling 95914 (ne). Steyermark & Nilsson 314 (ro). Steyermark & Rabe 96115 (ro). Steyermark & Steyermark 95406 (long); 95406-A (ne). Steyermark & Stoddart 118173-A (ne). Steyermark et al. 48744 (long); 51710 (long); 110227 (pter); 125086 (ne). Stolze 1487 (long); 1634 (hp). Stork 2263 (cont); 2658 (cont); 2722 (hp). Stübel 797 (ic).

Tonduz **9480** (lech). Torres 49 (cont). Tryon & Tryon 5330 (long).

Underwood 1315 (jam); 1613 (jam); 2036 (jam); 2696 (jam). Ule 68 (caud); **70** (caud & ulei); 187 (het). U.S. Expl. Exped. 23 (caud).

Valerio 295 (hp). van der Werff 3488 (ne); 7010 (mi). van der Werff & Gudiño 11125 (hp); 11169 (opaca); 11170 (pp). van der Werff & van Hardeveld 6762 (hp). van der Werff et al. 9566 (mi). Vásquez 188 (sord); 209 (kil); 245 (kil). Ventura A. 484 (long); 3306 (long); 3603 (long). Verleysen 174 (opaca). von Sneidern 5046 (lech). von Türckheim **1432** (sord); 3865 (long); 111691 (long).

Wacket 50 (tyu); 286 (caud); 21149 (tyu). Wagner **460** (pter); 1402 (het). Wagner & Gómez 79021a (hp). Wachter et al. 200 (long). Watt 82 (jam). Webster 13329 (ro); 13566 (ro); 13588 (ro). White & Lucansky 1968150 (cont); 1968174 (cont). Wilbur 7882 (ro). Wilbur & Stone 8919 (long). Wilson & Murray 563 (jam). Wright **1053** (hemip). Wurdack 2002 (pp).

Zak & Espinoza 5287 (opaca). Zak & Jaramillo 3635 (lech).

Index to Names

Accepted names are set in roman type; new taxa and combinations appear in boldface; all other names are italicized. In parentheses following an italicized name is the accepted taxon.

Aspidium Sw.
- *brachyneuron* Fée (tyucana)
- *caudatum*
  - var. *contractum* Christ (contracta)
- *imrayanum* (Hook.) Fée (rotundata)
- *rotundatum* Willd. (rotundata)

Cystopteris Bernh.
- *jamaicensis* Desv. (jamaicensis)

Dryopteris Adans.
- subg. *Stigmatopteris* (C. Chr.) C. Chr. (= Stigmatopteris) group *Peltochlaena* Fée ex C. Chr. excluded
  - *carrii* (Baker) C. Chr. (heterocarpa)
  - *caudata* (Raddi) C. Chr. (caudata)
  - *christii* C. Chr. (opaca)
  - *coalescens* (Baker) C. Chr. (opaca)
  - *cyclocolpa* (Christ) C. Chr. (lechleri)
  - *imrayana* (Hook.) Domin (rotundata)
  - *longicaudata* (Liebm.) Maxon (longicaudata)
  - *pellucidopunctata* C. Chr. (pellucidopunctata)
  - *prionites* (Kunze) C. Chr. (prioniodes)
  - *gemmipara* (C. Chr.) Maxon ex Proctor (gemmipara)
  - *hemiptera* (Maxon) C. Chr. (hemiptera)
  - *heterophlebia* (Baker) C. Chr. (heterophlebia)
  - *ichthiosma* (Sodiro) C. Chr. (ichthiosma)
  - *longipetiolata* C. Chr. (ichthiosma)
  - *nothochlaena* Maxon (jamaicensis)
  - *paucinervata* C. Chr. (opaca)
  - *prasina* (Baker) C. Chr. (lechleri)
  - *rotundata* C. Chr. (rotundata)
  - *sordida* Maxon (sordida)
  - *sylvicola* (Baker) C. Chr. (michaelis)
  - *tijuccana* C. Chr. (tyucana)
  - *ulei* (Christ) C. Chr. (ulei)

Meniscium Schreber
- *opacum* Baker (opaca)

Nephrodium Michaux
- *imrayanum* Hook. (rotundata)

Phegopteris Fée
- *brevinervis* Fée (brevinervis)
- *flavopunctata* (Kaulf.) Fée (rotundata)

denticulata Fée (prionites)
heterocarpa Fée (heterocarpa)
lechleri Mett. (lechleri)
macrophylla (Hook.) J. Smith (pellucidopunctata)
oligophlebia Salmon (opaca)
opaca (Baker) Christ (opaca)
perforata Fée uncertain
tenuis Fée (tyucana)
ulei Christ (ulei)

Polypodium L.
alloëopterum Kunze uncertain
carrii Baker in Mart. (heterocarpa)
caudatum Raddi (caudata)
caudatum Kaulf. (caudata)
coalescens Baker (opaca)
cyclocolpon Christ (lechleri)
dentatum Baker (ichthiosma)
flavopunctatum Kaulf. (rotundata)
heterophlebium Baker (heterophlebia)
ichthiosmum Sodiro (ichthiosma)
longicaudatum Liebm. (longicaudata)
macrophyllum Hook. (pellucidopunctata)
michaelis Baker (michaelis)
nephrodioides Klotzsch (nephrodioides)
oligophlebium Baker in Hook. & Baker (opaca)
prasinum Baker (lechleri)
prionites Kunze (prionites)
punctatum Spruce in Hook. (lechleri)
sylvicolum Baker (michaelis)
tyucanum Raddi (tyucana)

Stigmatopteris C. Chr.
alloëoptera (Kunze) C. Chr. uncertain
bradei Rosenstock (brevinervis)
brevinervis (Fée) R. C. Moran
bulbifera R. C. Moran
carrii (Baker) C. Chr. (heterocarpa)
caudata (Raddi) C. Chr.
chimalapensis Mickel & Beitel
clypeata (Maxon & C. Morton) Lellinger excluded
contracta (Christ) C. Chr.
cyclocolpa (Christ) C. Chr. (lechleri)
ecuadorensis C. Chr. (lechleri)
gemmipara C. Chr.
guianensis (Klotzsch) C. Chr. excluded
hemiptera (Maxon) C. Chr.
heterocarpa (Fée) Rosenstock
  var. *basilaris* Rosenstock (heterocarpa)
heterophlebia (Baker) R. C. Moran
ichthiosma (Sodiro) C. Chr.
jamaicensis (Desv.) Proctor
killipiana Lellinger
lechleri (Mett.) C. Chr.
litoralis Rosenstock (sordida)
longicaudata Liebm.
meniscioides Kramer in Kramer & van Donselaar excluded
michaelis (Baker) C. Chr.
nephrodioides (Klotzsch) C. Chr.
nothochlaena (Maxon) C. Chr. (jamaicensis)
opaca (Baker) C. Chr.
palmensis Rosenstock (longicaudata)
paludosa (C. Morton) R. Tryon & A. Tryon excluded
pellucidopunctata (C. Chr.) C. Chr.
prasina (Baker) C. Chr. (lechleri)
prionites (Kunze) C. Chr.
  var. *denticulata* (Fée) C. Chr. (prionites)
pterorhachis R. C. Moran
rotundata (Willd.) C. Chr.
  var. *trinidadensis* C. Chr. (rotundata)
sancti-gabrieli (Hook.) C. Chr. excluded
sordida (Maxon) C. Chr.
tyucana (Raddi) C. Chr.
ulei (Christ) Sehnem
varians (Fée) Alston excluded

ESTUDIOS MORFOLOGICOS EN EL SUBGENERO *DICHANTHELIUM* DE *PANICUM* (POACEAE: PANICOIDAE: PANICEAE), CON ESPECIAL REFERENCIA A *PANICUM SABULORUM*[1]

Osvaldo Morrone[2] *y Fernando Zuloaga*[2]

Resumen

El subgénero *Dichanthelium* fue establecido por Hitchcock & Chase (1910) en su tratamiento de las especies norteamericanas de *Panicum*. Estos autores definieron a *Dichanthelium* por poseer una roseta invernal de hojas cortas y anchas; en primavera las cañas son simples, con una inflorescencia terminal casmógama. Luego, nuevas cañas aparecen en la axila de las cañas principales y dan lugar a nuevas inflorescencias axilares con flores cleistógamas, repitiéndose este proceso durante el verano. En el presente tratamiento se ha tratado de establecer la variación existente en los caracteres anteriormente mencionados, para las especies sudamericanas de *Dichanthelium*, habiéndose realizado estudios morfológicos y anatómicos en diferentes poblaciones de *Panicum sabulorum* Lam., especie sudamericana de *Dichanthelium*, analizando el patrón de crecimiento, casmogamia y cleistogamia, presencia de glándulas, anatomía y relaciones de la especie con especies norte y sudamericanas del género.

Abstract

Subgenus *Dichanthelium* was established within *Panicum* by Hitchcock & Chase (1910) in their treatment of the North American species of the genus. These authors defined *Dichanthelium* as having an overwintering rosette of short, broad leaves; in spring the culms are simple, with a terminal, chasmogamous inflorescence. Later, branch culms arise at the nodes of the vernal culms, forming loose to rather dense fascicles of reduced leaves and branches with cleistogamous inflorescences. In the present treatment, variation of these characters was analyzed in South American species of *Dichanthelium*. Morphological and anatomical studies of different populations of *Panicum sabulorum* Lam., a South American species of subg. *Dichanthelium*, were carried out, examining the growth patterns, anatomy, and relationships of this species with other American species of the subgenus.

El subgénero *Dichanthelium* A. Hitchc. et Chase fue establecido por Hitchcock & Chase (1910) en su tratamiento de las especies norteamericanas del género *Panicum*. Estos autores definieron a *Dichanthelium*, sobre la base de especies de América del Norte, por poseer en la temporada invernal una roseta basal de hojas cortas y anchas; en la primavera las cañas son simples y llevan una inflorescencia terminal. Luego, numerosas ramificaciones nacen en los nudos inferiores de dicha caña, dando lugar a densos fascículos de hojas reducidas e inflorescencias menores, disminuyendo con el tiempo el tamaño de las ramificaciones, hojas e inflorescencias (Fig. 1). Hitchcock & Chase (1910) indicaron que las inflorescencias terminales llevaban espiguillas casmógamas, que raramente producían semillas viables, y las inflorescencias axilares llevaban espiguillas con flores cleistógamas, con una alta producción de semillas viables.

Hitchcock & Chase (1910) mencionaron ciertas excepciones dentro del subgénero en los caracteres anteriormente descritos, como por ejemplo la ausencia de roseta invernal en especies del Grupo Depauperata y de roseta y forma otoñal, es decir

[1] Deseamos expresar nuestro agradecimiento a Gerrit Davidse por la lectura crítica del manuscrito. El trabajo de campo en Colombia y Venezuela fue realizado con un subsidio de la National Geographic Society, #3964-88. Zuloaga desea expresar su agradecimiento a la Fundación Guggenheim por la beca otorgada para desarrollar sus investigaciones en el Missouri Botanical Garden, donde la presente revisión ha sido concluida. Ejemplares de herbario de *Panicum sabulorum* fueron examinados de los siguientes herbarios: BAA, CTES, G, HB, K, LIL, M, MO, NY, P, R, RB, SI, SP, US, W.

[2] Instituto de Botánica Darwinion, Casilla de Correo 22, San Isidro (1642), Argentina. Zuloaga está actualmente asociado al Missouri Botanical Garden.

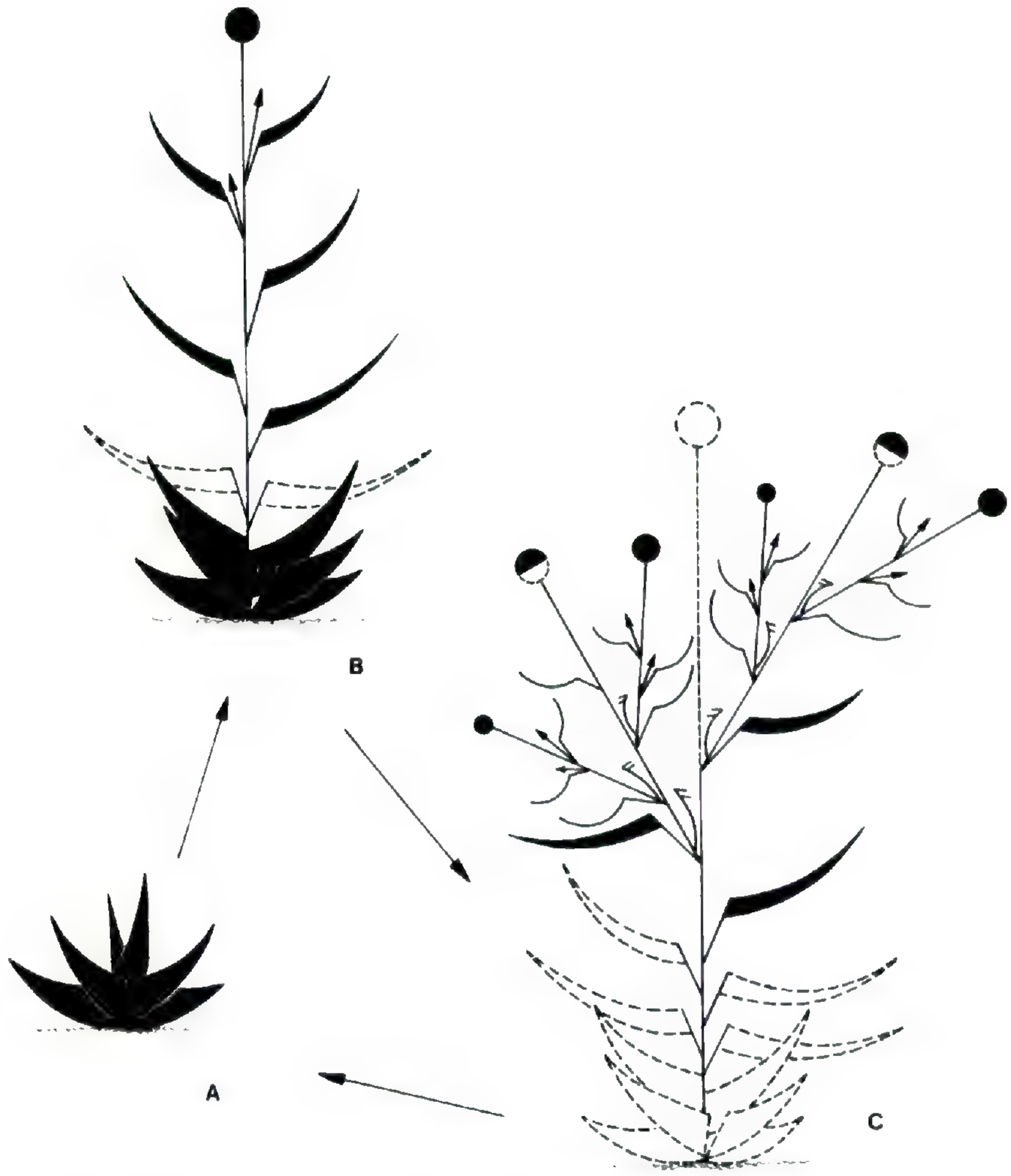

FIGURA 1. Esquema del desarrollo de una especie norteamericana del subgénero *Dichanthelium*.—A. Forma invernal.—B. Forma primaveral.—C. Forma otoñal. Círculos negros: inflorescencias en floración. Círculos negros y blancos: inflorescencias parcialmente en floración. Círculos con línea interrumpida: inflorescencias sin espiguillas (ya caídas). El tamaño de los círculos indica el orden de floración de las panojas.

sin cañas fasciculadas claramente desarrolladas en *Panicum viscidellum* Scribner. Estos autores tambien indicaron que "there is an intermediate stage of branching, in which the plants do not show the characteristic vernal nor autumnal habit. Vernal culms are sometimes produced on plants during the branched condition, because of renewal of activity, due to increased moisture, excess of nutriment, injury, or other causes" (Hitchcock & Chase, 1910: 142).

Gould (1974) elevó *Dichanthelium* a la categoría de género, y otros autores, como Clark & Gould (1975), Brown & Smith (1975), Gould & Clark (1978), y Gould (1980), apoyaron dicha segregación en base a los caracteres exomorfológicos previamente descritos, tipo fotosintético y ornamentación del antecio superior.

Todos los autores anteriormente mencionados basaron sus revisiones en especies de América del Norte de *Dichanthelium*, indicando que este taxon estaba representado por pocas especies en América del Sur. Más recientemente Lelong (1984), Clayton & Renvoize (1986), Zuloaga (1987) y Webster (1988) consideraron a *Dichanthelium* como un subgénero de *Panicum*, señalando que no existen caracteres suficientes para mantener a *Dichanthelium* como un género aparte.

Durante una revisión de las especies centro y sudamericanas de *Dichanthelium* (Zuloaga et al., en prep.), se comprobó que este subgénero está ricamente representado en el área, con cerca de 40 especies; además, estas especies tienen un mayor grado de variación morfológica en relación a las especies norteamericanas. Consecuentemente, se ha tratado de establecer en el presente trabajo la relación existente entre las especies norte y sudamericanas de *Dichanthelium*, considerando la validez de los caracteres morfológicos empleados hasta el momento para su segregación a nivel genérico o infragenérico. Se seleccionó, dentro de los taxa sudamericanos a *P. sabulorum* Lam., especie con la distribución más austral, y consecuentemente con mayores adaptaciones a climas más fríos. Estudios anatómicos y exomorfológicos fueron realizados en diferentes poblaciones de *P. sabulorum*, analizando el patrón de crecimiento ve-

getativo y florífero, cleistogamia y casmogamia, presencia de glándulas, ornamentación del antecio superior y caracteres histofoliares.

Materiales y Métodos

Especímenes de *Panicum sabulorum* fueron coleccionados en las provincias de Buenos Aires, Entre Ríos, Corrientes y Misiones (Argentina), y en Uruguay. El material fue herborizado y los ejemplares depositados en SI. Observaciones de las plantas vivas fueron realizadas en su ambiente natural entre 1987 y 1990. Plantas vivas fueron coleccionadas y mantenidas bajo cultivo en el invernáculo del Instituto Darwinion.

Las fotografías de campo fueron tomadas con una cámara Asahi Pentax usando una película Kodak Panatomic, ASA 32.

Los materiales para estudios morfológicos y anatómicos, provenientes de las poblaciones estudiadas, fueron fijados en Etanol 70% (ver lista de especímenes estudiados).

Para los estudios histofoliares se empleó material fijado o proveniente de materiales de herbario recuperados y rehidratados con Contrad 70 (Schmid & Turner, 1977). Los cortes transversales fueron obtenidos a mano alzada, previamente tratados con FH 5% para remover la sílice. Las secciones fueron coloreadas con safranina-fast green al 1% y montadas en gelatina glicerina.

Las epidermis fueron preparadas siguiendo el método propuesto por Metcalfe (1960).

Para la detección de células silíceas y suberosas se empleó respectivamente Fenol líquido (Metcalfe, 1960) y Sudán III (Sass, 1940). Amiloplastos fueron coloreados con I_2KI (Sass, 1940). Para la detección de cristales se siguió el método de Sánchez & Casabona (1981).

Cortes seriados de glándulas fueron obtenidos con un micrótomo rotativo. El material fue deshidratado en una serie de alcoholes ascendentes e incluido en Paramat. Las secciones, de 8–12 μm de espesor, fueron coloreadas con safranina–fast green y montadas en bálsamo de Canadá.

El líquido secretado por las glándulas fue colectado por medio de un tubo micropilar y la presencia de azúcares testeada mediante la técnica colorimétrica propuesta por Dubois et al. (1956).

Para la detección de aceites se empleó Sudán IV (Jensen, 1962).

Las cañas, hojas y estructuras reproductivas fueron estudiadas con un microscopio estereoscópico Wild M5 y las preparaciones histológicas con un microscopio fotónico Wild M20.

Las microfotografías de glándulas y hojas fueron tomadas en un microscopio fotónico Zeiss.

Materiales de P. sabulorum empleados en los estudios anatómicos: ARGENTINA. BUENOS AIRES: Punta Lara, *Zuloaga & Deginani 3959, 3861* (SI); Escobar, Paraná de las Palmas, *Zuloaga & Morrone 4544* (SI); Escobar, *Zuloaga 3860* (SI). CORRIENTES: Ituzaingó, 20 km de Ituzaingó hacia el E, *Zuloaga et al. 3228, 3231* (SI). ENTRE RÍOS: Arroyo El Palmar, *Zuloaga & Morrone 3857* (MO, SI); Colonia Ayuí, *Zuloaga & Morrone 3852* (MO, SI); de Calabacilla a Nueva Escocia, *Zuloaga & Morrone 3846, 3847* (SI); de Ceibas a Médanos, 7 km de Médanos, *Zuloaga & Morrone 3840* (SI); ruta 12, desvío a Holt, Arroyo El Cuartillo, *Zuloaga 3864* (MO, SI). MISIONES: San Ignacio, casa de Horacio Quiroga, *Zuloaga et al. 3191* (SI); INTA, Cuartel Río Victoria, ruta nac. 14, aprox. 11 km de San Vicente, *Giberti & Daviña 210* (SI). BRASIL. RIO GRANDE DO SUL: Jaguarão, 8 km W de Jaguarão, *Allem & Vieira 1868* (SI); Pelotas, *Swallen 7137* (US); Santa Victoria do Palmar, *Swallen 7396* (US). RIO DE JANEIRO: Parque Nacional Itatiaia, Rio Campo Belo, *Zuloaga et al. 2361* (SI). SANTA CATARINA: 4 km S of Campo Alegre, *Smith & Klein 7334* (US). SÃO PAULO: São Paulo, Parque do Estado, *Sendulsky 1278* (SI). URUGUAY. CANELONES: Ruta Interbalnearia, km 51, Arroyo Solís Chico, *Dubcovsky 834, 835, 836, 837* (SI).

Hábitat

Panicum sabulorum posee una gran adaptabilidad para ocupar hábitats muy diversos, creciendo desde lugares húmedos y sombríos, en bordes o en el interior de bosques y selvas, hasta lugares más abiertos y soleados, en suelos usualmente arenosos y secos, estando presente también en suelos rocosos; a menudo es posible encontrar especímenes en areas perturbadas.

La morfología de los especímenes está correlacionada con el hábitat: plantas de lugares húmedos y sombríos son delicadas, apoyantes en la vegetación o decumbentes; generalmente poseen hojas, inflorescencias y espiguillas glabras (Fig. 2C). El tamaño de los ejemplares varía desde pequeños hasta otros que llegan a 80 cm de alto, con cañas apoyantes en la vegetación. Las poblaciones de lugares abiertos y soleados, y que crecen comúnmente en suelos arenosos, son plantas cespitosas, con hojas rígidas y pilosas, e inflorescencias y espiguillas pilosas (Fig. 2D), variando el tamaño desde especímenes pequeños a mayores, densamente ramificados (Fig. 2).

En condiciones de invernáculo las plantas provenientes de lugares abiertos y arenosos, con entrenudos muy cortos, producen durante la primavera cañas apoyantes, con entrenudos largos, hasta

FIGURA 2. Fotografías de campo de *P. sabulorum*. —A. Plántulas naciendo en primavera.—B. Innovaciones apareciendo en la base de la planta durante el verano (flecha).—C. Cañas densamente ramificadas y nuevas innovaciones, con hojas más anchas, en la base de la planta, durante el verano.—D. Planta de lugares arenosos, abiertos.—E. Cañas simples con inflorescencias terminales formadas durante el otoño.—F. Inflorescencias terminales sobre cañas con hojas rígidas.—G. Inflorescencia terminal (flecha) e inflorescencia axilar.—H. Planta ramificada con inflorescencia terminal (flecha) e inflorescencias axilares.

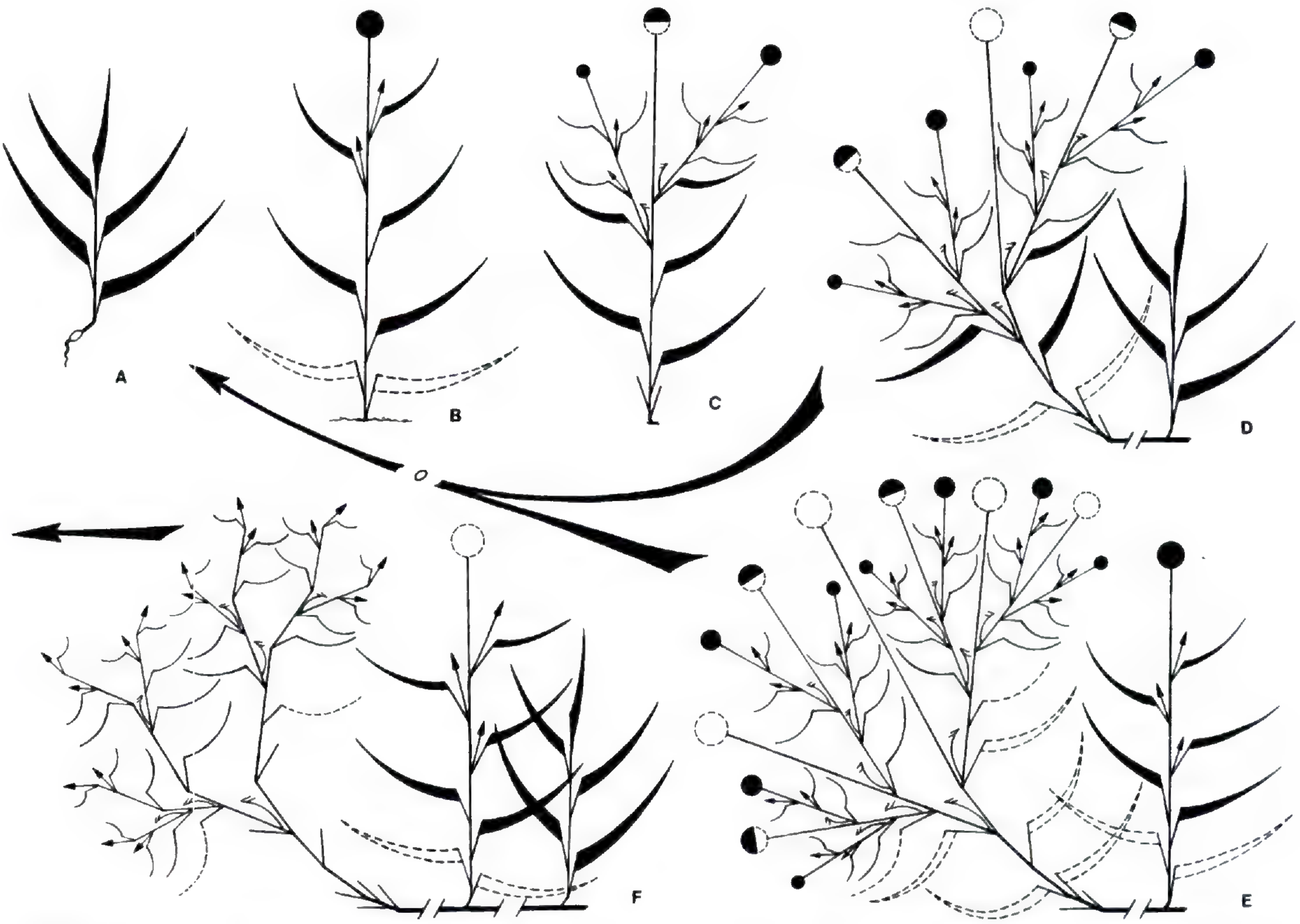

FIGURA 3. Esquema del desarrollo de *P. sabulorum*. Círculos negros: inflorescencias en floracion. Círculos negros y blancos: inflorescencias parcialmente en floracion. Círculos con línea interrumpida: inflorescencias sin espiguillas (ya caídas). Las flechas indican el desarrollo de las plantas, ya sea formando nuevos especímenes (a partir de semillas) o que la misma planta continúa el ciclo el siguiente año. El tamaño de los círculos indica el orden de floración de las panojas.

de 15 cm de largo, semejantes a los especímenes que crecen en lugares húmedos y sombríos.

MORFOLOGÍA, DESARROLLO Y RAMIFICACIÓN (FIGS. 2, 3)

El estudio de las poblaciones citadas durante los últimos cuatro años ha permitido observar un incremento en la complejidad de los ejemplares a medida que los mismos se desarrollan. En la primavera germinan nuevas plantas, las que desarrollan cañas simples y erectas, con entrenudos largos y hojas anchas, cordadas en la base (Fig. 2A).

Luego de formadas las primeras 7 u 8 hojas el crecimiento vegetativo cesa y se forma una inflorescencia terminal multiflora, la que emerge de un largo pedúnculo (Fig. 3B).

Con posterioridad a la floración de la panoja terminal, la caña principal comienza a ramificarse en los nudos superiores, observándose cañas axilares a fines de la primavera y comienzos del verano (Fig. 2C). Estas ramificaciones tienen 3 o 4 hojas reducidas, menores que las presentes originalmente en la caña principal, y terminan en inflorescencias axilares paucifloras. En este momento del desarrollo las inflorescencias axilares pueden coexistir con las inflorescencias terminales de la caña principal, o las inflorescencias terminales pueden encontrarse sin espiguillas (Fig. 3C).

La ramificación de las cañas continúa durante todo el verano, con inflorescencias laterales numerosas, existiendo una consecuente reducción de los entrenudos, hojas, e inflorescencias, lo que da a la planta un aspecto fasciculado. Asimismo, nuevas innovaciones aparecen en la base de la planta, siendo estas similares a las innovaciones primaverales, con cañas simples con hojas cordadas y anchas (Fig. 3D).

Al final del verano y comienzo del otoño continúa la profusa ramificación en las cañas, habiendo desaparecido en este punto las inflorescencias terminales primarias y las hojas basales anchas de dichas cañas primarias (Fig. 1C, 3E, láminas e inflorescencias faltantes indicadas con trazo discontínuo). Las cañas simples formadas en la fase anterior (Fig. 3D) florecen dando una inflorescencia terminal, para posteriormente comenzar a ramificarse en los nudos superiores (Fig. 3E).

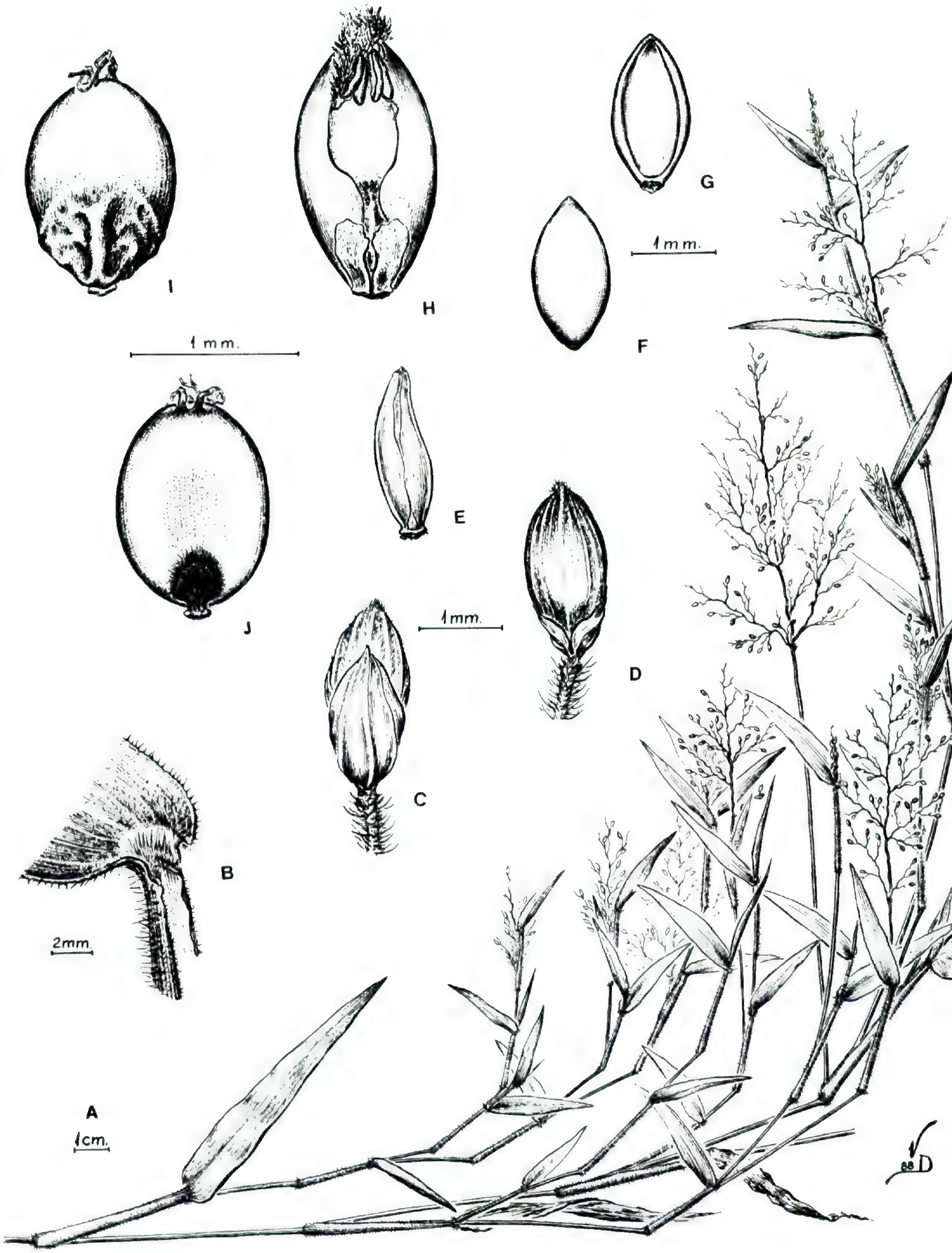

FIGURA 4. *Panicum sabulorum*. A. Hábito.--B. Lígula.—C. Espiguilla, vista ventral.—D. Espiguilla, vista dorsal.—E. Pálea inferior.—F. Antecio superior, vista dorsal.—G. Antecio superior, vista ventral.—H. Lemma superior con lodículas, cariopsis, estigma y anteras.—I. Cariopsis, visto del lado del embrión.—J. Cariopsis visto del lado del hilo (de *Zuloaga et al. 3191*, SI).

Las plantas mantienen durante el invierno la mayor parte de la porción aérea, con las cañas profusamente ramificadas, no formándose durante este lapso nuevas innovaciones. Al comienzo de la siguiente primavera, las cañas que permanecieron en la planta continúan ramificándose, formando pequeñas inflorescencias en el extremo de cada nueva ramificación (Fig. 3F). A la vez, nuevas

innovaciones aparecen en la planta, con cañas simples y hojas cordadas, anchas, lo que implica un nuevo comienzo del ciclo (Fig. 3F).

Debido a la profusa ramificación de las cañas, las mismas son decumbentes y generalmente apoyantes en la vegetación.

Plantas provenientes de poblaciones de Entre Ríos y Buenos Aires preservadas en invernáculo, mantuvieron durante el invierno una activa producción de ramificaciones laterales y muy frecuentemente de inflorescencias axilares. Esta actividad de los meristemas está directamente relacionada con la protección de las plantas a la rigurosidad del clima durante el invierno.

Espiguilla (Fig. 4)

La espiguilla posee una gluma inferior 3–5-nervia, que alcanza ½ o poco más del largo de la espiguilla, gluma superior y lemma inferior subiguales y 7–9-nervias, pálea inferior presente, flor inferior ausente y antecio superior endurecido, papiloso y con el ápice de la lemma cortamente mucronado.

Ocasionalmente se hallaron espiguillas trifloras en el material estudiado, con flor inferior neutra, con su correspondiente lemma, una flor intermedia hermafrodita con lemma y pálea endurecidas y una flor superior tambien hermafrodita con lemma y pálea endurecidas. Espiguillas trifloras han sido citadas previamente en el género *Panicum* (Palacios, 1968; Zuloaga & Sendulsky, 1988) y en el género *Lasiacis* (Davidse, 1978).

En espiguillas maduras se observó un eleosoma en la porción basal de la espiguilla, en la región periférica de la raquilla entre la inserción de la gluma inferior y la lemma inferior, hallándose aceite en las células. La presencia de eleosoma en gramíneas ha sido generalmente correlacionada con la mirmecofilia (Berg, 1985; Davidse, 1987).

El antecio superior en *P. sabulorum* es endurecido y biconvexo, liso y con papilas simples distribuidas en hileras longitudinales regulares, pudiendo observarse pelos y estomas en el ápice de lemma y pálea respectivamente.

Casmogamia y Cleistogamia (Tabla 1)

Las espiguillas que se disponen en las inflorescencias terminales y axilares son isomorfas, homógamas, no existiendo diferencias morfológicas entre las flores cleistógamas y casmógamas. Así, no se observaron diferencias en las anteras de flores casmógamas y cleistógamas, variando entre 0.3 a 1 mm de largo.

El análisis del material de *P. sabulorum* mostró que no existe una correlación entre inflorescencias terminales y flores casmógamas e inflorescencias laterales, o axilares, y flores cleistógamas. Espiguillas con flores casmógamas son frecuentes tanto en las inflorescencias terminales como en las laterales; espiguillas con flores cleistógamas son escasas y se pueden hallar en ambos tipos de inflorescencias y en cualquier momento del período de floración. Cuando presentes las espiguillas con flores cleistógamas se encuentran en inflorescencias que llevan también espiguillas con flores casmógamas.

Tabla 1. Porcentaje de espiguillas con cariopsis y flores cleistógamas y casmógamas en inflorescencias terminales y axilares.

	Total	%
Inflorescencia terminal (noviembre)		
Espiguillas con cariopsis	639	93.55
Espiguillas sin cariopsis	44	6.45
Flores casmógamas	489	99.59
Flores cleistógamas	2	0.41
Inflorescencias axilares (enero)		
Espiguillas con cariopsis	100	86.9
Espiguillas sin cariopsis	15	13.1
Flores casmógamas	100	86.9
Flores cleistógamas	15	13.1

El estudio de 683 espiguillas maduras en inflorescencias terminales permitió confirmar que el 93.5% de las mismas forman cariopsis. Además, sobre 491 espiguillas de inflorescencias terminales producidas en noviembre se estableció que el 99.59% de las espiguillas son casmógamas.

Observaciones realizadas en 115 espiguillas provenientes de inflorescencias axilares permitió determinar que el 86.9% producen cariopsis y un mismo porcentaje corresponde a espiguillas casmógamas.

La variación en la presencia de flores cleistógamas en las inflorescencias terminales y axilares de *P. sabulorum* posiblemente esté condicionada por factores ambientales, por lo que la cleistogamia podría ser clasificada como facultativa (Connor, 1979).

Glándulas (Fig. 5)

Nectarios extraflorales han sido citados ocasionalmente para la familia Poaceae, como por ejemplo en trabajos de Bowden (1971), Davidse (1988), Fahn (1979), Mattei & Tropea (1908, 1909), Nicora (1941), Reeder & Toolin (1989), y Linder & Ellis (1990). Pelos glandulares multicelulares han sido mencionados en especies de la sección *Clavelligera* Stapf de *Panicum* (Kabuye & Wood, 1969) y glándulas crateriformes para la lemma inferior de especies de la sección *Stolonifera* (A.

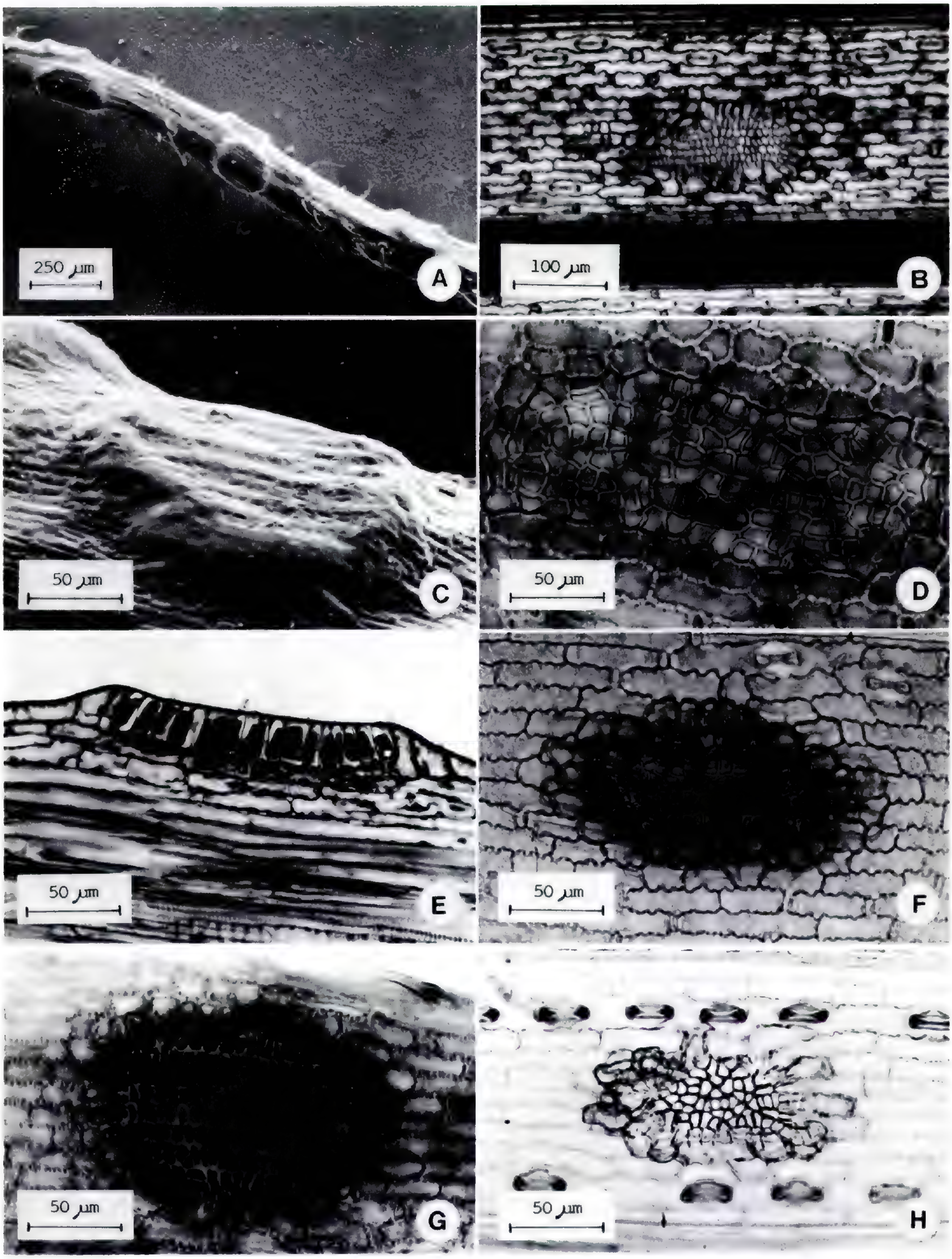

FIGURA 5. A–C, E, G. Fotomicrografías de glándulas de *P. sabulorum*. —A. Eje de la inflorescencia.—B. Glándula en vaina.—C. Glándula en eje de la inflorescencia.—E. Corte longitudinal de glándula en eje de la inflorescencia.—G. Glándula en eje de la panoja—D. Fotomicrografía de glándula de la vaina de *P. surrectum*. F, H. Fotomicrografías de glándulas de *P. adenorhachis*. —F. Glándula en vaina.—H. Glándula en lámina (A–C, E, G, de *Zuloaga y Morrone 3544*, SI; D, de *Chase 9555*, US; F, H, de *Mori et al. 12451a*, US).

Hitchc. & Chase) Pilger por Zuloaga & Sendulsky (1988).

Glándulas multicelulares secretoras fueron observadas sobre pedúnculos, ramas de la inflorescencia (Fig. 5A, C, E, G), pedicelos, y en entrenudos o vainas (Fig. 5B), de numerosos especímenes de *P. sabulorum*. La presencia de dichas glándulas es marcadamente variable, hallándose una gradación desde ejemplares con abundantes glándulas a otros con una menor densidad, o ausentes.

Las glándulas son más frecuentes en las inflorescencias y su presencia es más notoria al comienzo de la primavera sobre las inflorescencias terminales, siendo raras, o ausentes, en las inflorescencias que se forman durante el verano y el otoño.

Las glándulas son sésiles, crateriformes, y de forma anular o elipsoide, midiendo de 0.15–0.3 mm de largo por 0.1–0.16 mm de ancho. Sobre la superficie glandular es posible observar a trasluz pequeñas gotitas brillantes; la mayor producción glandular se da por la mañana y al atardecer, decreciendo a medida que el organo envejece.

El tejido secretor se halla ubicado en la depresión de la glándula. En vista paradermal las células secretoras son cuadradas en contorno, más pequeñas que las células epidérmicas vecinas, de paredes anticlinales lisas, rectas y engrosadas, semejando el tejido a una rejilla (Fig. 5B, C; Fig. 6). Las células epidérmicas que rodean al tejido glandular son de contorno rectangular y se hallan realzadas en relación al resto de la epidermis.

El tejido glandular es unistratificado en corte transversal y está restringido a la epidermis (Fig. 5E). Está compuesto por un número variable de células prismáticas, alargadas transversalmente, en empalizada y sin espacios intercelulares. Las células tienen aproximadamente 25 μm de largo en corte transversal y longitudinal y poseen paredes delgadas a excepción de las paredes radiales, las que tienen un conspícuo espesamiento junto a la pared tangencial externa. El citoplasma es denso y granuloso y se tiñe intensamente, con un gran nucleo junto a la pared tangencial interna. La cutícula es delgada y fuertemente cutinizada en las células epidérmicas que la rodean (Fig. 5E).

Las glándulas carecen de tejido vascular, y el estrato subepidérmico asociado al tejido glandular está constituido por células parenquimáticas, rectangulares en corte longitudinal e isodiamétricas en corte transversal, de paredes lisas y con pocos o sin cloroplastos.

El análisis cualitativo del líquido secretado por las glándulas multicelulares, a traves de un ensayo con fenol-ácido sulfúrico (Dubois et al., 1956), permitió detectar la presencia de azúcares. Esto permite inferir que las glándulas funcionan como nectarios extraflorales.

La función de los nectarios extraflorales en *P. sabulorum* no es conocida. Bentley (1976), Elias & Gelband (1976, 1977), sostienen que los nectarios extraflorales atraerían a las hormigas, protegiendo a las plantas del ataque de herbívoros. Davidse (1988) citó que las glándulas presentes en *Pentastichis* podrían ser parte de un mecanismo de defensa contra los herbívoros. En las poblaciones aquí analizadas de *P. sabulorum* no se observó interacción entre hormigas y plantas con nectarios extraflorales.

Los nectarios presentes en *P. sabulorum* difieren de los pelos glandulares citados para la sección *Clavelligera* por Kabuye & Wood (1969) por ser estos últimos pedicelados. A su vez, son aparentemente similares a los citados para espiguillas de especies de la sección *Stolonifera* por Zuloaga & Sendulsky (1988), no habiendo estos últimos autores estudiado en detalle dichas glándulas.

Glándulas similares a las presentes en *P. sabulorum* han sido detectadas, dentro del subgénero *Dichanthelium*, en especies norte y sudamericanas, como por ejemplo *P. adenorhachis* Zuloaga & Morrone (Fig. 5F, H), *P. stigmosum* Trin., *P. sphaerocarpon* Elliott, *P. strigosum* Muhl., *P. scoparium* Lam. y *P. surrectum* Chase ex Zuloaga & Morrone (Fig. 5D).

Caracteres Histofoliares (Fig. 6)

Epidermis abaxial. *Zonas costales* angostas de 3–6 hileras de células de ancho; cuerpos silíceos halteriformes. *Zonas intercostales* conspícuas, de 10–14 hileras de células; células largas cercanas a las zonas costales rectangulares, tres veces más largas que anchas, con paredes anticlinales longitudinales onduladas; células largas de la región intercostal media cuadradas a poligonales, con paredes sinuosas a casi paralelas. Células intercostales cortas rectangulares, alargadas transversalmente y con paredes sinuosas, solitarias o en pares, separadas por una o más celulas largas. *Aparatos estomáticos* con células subsidiarias angostamente triangulares, dispuestos en 2 hileras a cada lado de la zona costal, de 28.5–49.5 μm de largo por 20–26 μm de ancho, alternando con células interestomáticas; células interestomáticas con paredes anticlinales transversales cóncavas. *Micropelos* bicelulares, de 41.5–74.5 μm de largo, célula basal de paredes paralelas, de tamaño igual o menor que la célula distal; célula distal fusiforme, aguda y con paredes más delgadas que las de la célula basal.

FIGURA 6. A–D. Anatomía de *P. sabulorum*. —A, C. Corte transversal. —B, D. Epidermis abaxial. E, F. Anatomía de *P. acuminatum*. —E. Corte transversal. —F. Epidermis abaxial (A, B de *Zuloaga & Morrone 4544*, SI; C, D de *Zuloaga & Morrone 3840*, SI; E, F de *Zuloaga 2490*, SI).

Macropelos presentes o ausentes, cuando presentes en las zonas intercostales, unicelulares y de paredes gruesas, agudos y con la base bulbosa hundida en el mesófilo. *Aguijones* no vistos. *Papilas* ausentes.

Lámina en corte transversal. Transcorte plano de 170–360 µm de espesor. Costillas conspícuas en la cara adaxial, dispuestas sobre todos los haces vasculares, surcos adaxiales poco marcados ⅓ del ancho de la lámina; costillas y surcos inconspícuos en la cara abaxial. Nervio medio inconspícuo, con un haz vascular primario indistinguible estructuralmente de los laterales; 2–5 haces vasculares de segundo orden entre haces vasculares de primer orden contíguos; haces vasculares contíguos separados por 5–8 células del mesófilo, a una distancia de 195–265 µm entre haces contíguos. *Haces vasculares de primer orden* trabados, de contorno circular, rodeados por dos vainas; vaina

externa parenquimática completa, formada por 15–18 células globosas, vacías o con escasos cloroplastos no especializados; extensiones de la vaina parenquimática presentes hacia ambas epidermis, con 1–3 columnas de células; vaina interna mestomática completa. *Haces vasculares de segundo orden* trabados, de contorno poligonal; vaina externa parenquimática completa, formada por 6–10 células globosas; extensiones de la vaina parenquimática en una o dos columnas, cada columna con 3–7 células hacia la cara adaxial, y con 2–4 células hacia la cara abaxial. *Clorénquima* irregularmente radiado alrededor de los haces vasculares, células tabulares, raquimorfas, espacios aéreos intercelulares numerosos. *Células buliformes* en abanico, dispuestas en grupos regulares de 3–5 células en los surcos adaxiales. Células epidérmicas abaxiales, opuestas a las células buliformes, globosas, de mayor tamaño que las adyacentes a la zona intercostal. Amiloplastos presentes en las células clorenquimáticas.

OBSERVACIONES

Se ha observado una correlación entre los caracteres exomorfológicos y el hábitat de las plantas con los caracteres histofoliares. Ejemplares que crecen en ambientes húmedos y sombríos, con espiguillas pequeñas y glabras, usualmente poseen láminas delgadas, de 170–230 μm de espesor, estomas pequeños de 28.5–44.1 μm de largo, y epidermis con macropelos aislados a frecuentes. Las plantas que habitan en lugares abiertos, arenosos y drenados, y que generalmente tienen espiguillas mayores y pilosas, poseen láminas más gruesas, de 220–360 μm de espesor, estomas mayores, de 33.70–49.5 μm de largo, y macropelos abundantes.

Micropelos 3-celulares fueron observados en el ejemplar *Giberti y Daviña 210*. Estos micropelos son fusiformes, con la célula basal de paredes más engrosadas que la célula media y distal. Pelos multicelulares fueron previamente reportados para la tribu Paniceae en *Paspalum* (Türpe, 1966) y *Panicum validum* Mez (Zuloaga et al., 1989).

Discusión

El estudio morfológico de *P. sabulorum* y especies afines de América del Sur, como por ejemplo *P. superatum*, *P. stigmosum*, y *P. surrectum* ha confirmado la variación existente en los caracteres tradicionalmente utilizados para distinguir a *Dichanthelium* a nivel genérico o infragenérico.

ROSETA BASAL

La roseta basal, propia de las especies norteamericanas, no se observa en *P. sabulorum* o en las restantes especies de *Dichanthelium* que crecen en México, Mesoamérica y América del Sur. Así por ejemplo en *P. sphaerocarpon*, *P. acuminatum* Sw., y *P. aciculare* Desv. ex Poiret, especies comunes en América del Norte y con una morfología similar al resto de las especies del subgénero que crecen en el área, no se forma una roseta basal en las plantas que habitan en Meso y Sudamérica. Una excepción se da en especímenes de *P. aciculare* coleccionados en Cuba y de *P. scoparium* de la República Dominicana, en los que se observa una roseta basal; en este caso se podría sugerir que las especies se introdujeron en las Indias Occidentales desde los Estados Unidos y mantienen, en determinados casos, especializaciones como el poseer roseta basal.

RAMIFICACIONES

El patrón de ramificación presente en *P. sabulorum* concuerda con el que se halla en las especies norteamericanas del género, como así también en las restantes especies sudamericanas de *Dichanthelium*.

Cabe destacar la persistencia de las cañas durante la temporada invernal, y la posterior formación de nuevas ramificaciones, e inflorescencias, a partir de las mismas durante la primavera siguiente.

La ausencia de roseta basal y permanencia de las cañas, con una eventual producción de espiguillas, puede explicarse por la ausencia de inviernos rigurosos tanto en Mesoamérica como en América del Sur.

DIMORFISMO FOLIAR

El dimorfismo foliar, con hojas de tamaño diferente en las cañas simples y ramificadas, sólo se halla presente en especies de distribución boreal y en *P. sabulorum*, siendo esta última la especie del subgénero *Dichanthelium* con distribución más austral en América del Sur. En el resto de las especies de *Dichanthelium* las cañas principales se encuentran ramificadas, llevando las ramificaciones hojas de tamaño similar a las de la caña principal.

Durante el presente estudio se comparó el patrón de ramificación y dimorfismo foliar con las restantes especies de *Dichanthelium* que crecen en América del Sur, en particular con aquellas que

habitan desde América del Norte hasta Colombia y Venezuela. Se analizó material, en vivo y de herbario, de *P. acuminatum*, *P. aciculare* y *P. sphaerocarpon*, proveniente de Colombia y Venezuela; este material no presenta ningún tipo de dimorfismo foliar ni roseta basal, caracteres que sí se hallan presentes en especímenes de estas especies de América del Norte.

CASMOGAMIA Y CLEISTOGAMIA

El porcentaje de flores cleistógamas en las inflorescencias es muy bajo o nulo en las especies sudamericanas de *Dichanthelium* y mayor en las especies que crecen en América del Norte. Esta variación ha sido corroborada en la presente contribución mediante el estudio de especies norteamericanas de *Dichanthelium* que llegan hasta América del Sur, como por ejemplo *P. aciculare*, *P. acuminatum* y *P. sphaerocarpon*. En el material analizado de estos taxa, coleccionado en Colombia y Venezuela, se hallaron pocas flores cleistógamas.

La presencia o ausencia de flores cleistógamas está directamente relacionada, tal como ocurre con los caracteres vegetativos, con la adaptación de las plantas a condiciones ambientales desfavorables.

ANATOMÍA FOLIAR

El análisis de la estructura histofoliar de *P. sabulorum*, y especies de la sección *Dichanthelium*, permitió concluir que esta sección posee una serie de caracteres histofoliares comunes, siendo todas sus especies no-Kranz, con clorénquima irregularmente radiado alrededor de los haces vasculares, con más de 4 células entre haces vasculares adyacentes, usualmente de 5 a 8 células; células de la vaina parenquimática de los haces vasculares sin cloroplastos especializados, presencia de almidón en las células clorenquimáticas, y conspícuas extensiones parenquimáticas de la vaina externa hacia ambas epidermis. En la epidermis se observan estomas con células subsidiarias triangulares a cupuliformes, y micropelos 2-celulares, fusiformes, con la célula basal igual o mayor que la distal, y célula distal atenuada o aguda.

ORNAMENTACIÓN DEL ANTECIO SUPERIOR

El antecio superior de *P. sabulorum* comparte las características presentes en el resto de especies del subgénero, con papilas en la superficie y lemma comúnmente apiculada o mucronada y con estomas hacia su ápice.

CONCLUSIONES

El estudio efectuado en poblaciones de *P. sabulorum*, y en otras especies del subgénero *Dichanthelium*, sección *Dichanthelium*, de Mesoamérica (Zuloaga et al., en prep.) permite concluir que los caracteres tradicionalmente utilizados para distinguir a *Dichanthelium* no se mantienen constantes dentro del subgénero. Dichos caracteres, presencia de roseta basal, dimorfismo foliar y casmogamia y cleistogamia, representarían una estrategia evolutiva de las plantas a climas más rigurosos. El hecho de que las especies que crecen en América del Norte posean caracteres adaptativos más especializados, y la existencia de un alto número de especies diploides del súbgenero en America del Sur (Dubcovsky & Zuloaga, en prep.) permite sugerir que este grupo tiene, contrariamente a lo sustentado anteriormente por Hitchcock & Chase (1910), Brown (1948) y Gould & Shaw (1983), su centro de origen en América del Sur, desde donde radió hacia América del Norte, adquiriendo formas morfológicas evolucionadas, distribuyéndose ampliamente al adaptarse a climas con una estación invernal marcada.

Los resultados del presente trabajo nos permiten concluir que no existen caracteres suficientes para mantener a *Dichanthelium* como un género separado de *Panicum*. Dentro de *Panicum* el subgénero *Dichanthelium* se distingue de los restantes subgéneros por una suma de caracteres, incluyendo (además de la presencia o ausencia de roseta basal, dimorfismo y cleistogamia, ya citados previamente) el que poseen por lo general inflorescencias laxas, difusas, con espiguillas usualmente elipsoides a obovoides, gluma superior y lemma inferior usualmente 7–9-nervias, antecio superior papiloso, con papilas simples distribuidas regularmente, cortamente mucronado o apiculado en el ápice, y tipo fotosintético y anatómico no-Kranz, con extensiones de la vaina parenquimática hacia ambas epidermis.

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A REVISION OF *RADDIELLA* (POACEAE: BAMBUSOIDEAE: OLYREAE)[1]

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Abstract

Raddiella is a genus of seven species of low- to mid-elevation, small herbaceous bamboos (Poaceae: Bambusoideae: Olyreae) that occurs from Panama and Trinidad to Bolivia and Brazil. *Raddiella esenbeckii* is widespread in savannas and cerrados, but its six congeners are rare, and many occur only on wet rocks in the spray zone below waterfalls. The new Brazilian species, *R. minima*, with the smallest leaves of any bambusoid grass, and *R. lunata*, with lunate female florets, are described. This first revision of *Raddiella* includes a key to the recognized species, descriptions, and distribution maps, as well as scanning electron micrographs of the female florets, which reveal taxonomically important interspecific differences.

Along with the Cuban genus *Mniochloa* Chase, members of *Raddiella* Swallen (Poaceae: Bambusoideae: Olyreae) are the smallest bambusoid grasses in the world. The genus was described (Swallen, 1948) on the basis of three species, *Raddiella nana* (Doell) Swallen (= *R. esenbeckii* (Steudel) Calderón & Soderstrom), the type species; *R. truncata* Swallen (= *Parodiolyra lateralis* (Nees) Soderstrom & Zuloaga); and *R. malmeana* (E. Ekman) Swallen. Swallen characterized the genus as monoecious with the male and female spikelets in different inflorescences; the pedicels of female spikelets not conspicuously thickened upwards; female spikelets with the glumes 3-nerved, and the floret indurate, white, and smooth.

Soderstrom (1965) described three new species of *Raddiella*, *R. kaieteurana*, *R. maipuriensis*, and *R. potaroensis*, and included a key to the six species in the genus. Later, based on priority, Calderón & Soderstrom (1980) considered *R. esenbeckii* as the valid name for the type species of the genus and transferred *Panicum molliculmum* Swallen to *Raddiella* (as *R. molliculma*).

Examination of more herbarium material since Soderstrom's summary of the genus has revealed two distinctive new species of *Raddiella*, and a scanning electron microscope study of female florets has proven useful in clarifying species limits, warranting the following revision of the genus.

Material and Methods

Classical alpha taxonomic methods were used to study *Raddiella*. In addition, scanning electron micrographs were made of the female florets of a few populations of each of the species except *R. minima*, using the same procedures and equipment as described by Soderstrom & Zuloaga (1989). The vouchers for this study are marked with an asterisk (*) in the lists of specimens examined in the taxonomic treatment.

Morphology

Species of *Raddiella* are remarkable in the Bambusoideae for their very small size. Most species appear to be annuals and represent the only annual bambusoids, excluding oryzoids. Many are obligate phreatophytes, growing only on wet rocks in the constantly moist spray zone of riversides below waterfalls; exceptions are the perennials *R. esenbeckii* and possibly *R. minima*, which often grow in dry savannas and cerrados. *Raddiella esenbeckii* and possibly *R. minima* are also unique in the genus in exhibiting nyctinasty, or sleep movements, the blades folding upwards at night or under water stress. The blades are firm and conspicuously asymmetrical in *R. esenbeckii* and *R. minima*, thinly membranous and only slightly asymmetrical in the other species.

[1] We are grateful to Vladimiro Dudás and Bruno Manara for the illustrations, to Bruno Manara for assistance with the Latin diagnoses, and to Gerrit Davidse, Lynn Clark, Edgardo Romero, Mary Sangrey, and the late Thomas R. Soderstrom for help in various ways. The first author expresses gratitude to the Guggenheim Foundation for a fellowship that allowed him to work on this research at the Missouri Botanical Garden. Figure 13A–G is used with permission of Paul E. Berry, editor of the *Flora of the Venezuelan Guayana*.

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Species of *Raddiella* bear terminal and numerous axillary inflorescences; both types are contracted, few-flowered, and barely exserted from the leaf sheaths. The several inflorescences arising from the uppermost node each consist of several (rarely one as in *R. minima*) early-deciduous male spikelets on short, filiform pedicels. Several axillary inflorescences occur at each node, and the disposition of spikelets in these is more variable. Typically, the entire inflorescence is female, with spikelets borne on short, filiform pedicels. However, at a given node, inflorescences bearing 1–2 terminal female spikelets as well as 1–several short-pedicelled male spikelets positioned below them can be found. Exceptions to these patterns include *R. molliculma*, in which both terminal and axillary inflorescences are long-peduncled and each consists of 1–2 terminal male and 1–2 subterminal female spikelets; and *R. lunata*, with racemose-appearing inflorescences that may be up to 12-flowered, but in which the disposition of the sexes in the single, overly mature specimen is not entirely clear.

The spikelets of *Raddiella* are fairly typical of those of other olyroid genera. In the female spikelets, the glumes vary from persistent in *R. esenbeckii* and *R. minima*, to deciduous together with the floret in the other species. The glumes are 3–5-nerved, and there is a characteristic indurate, thickened, interglumal internode present. The female floret morphology is ellipsoidal in all species (Fig. 13) except for *R. lunata*, which has curious, lunate (crescent-shaped in profile) florets that taper to an acute point at both ends (Fig. 14). Floret epidermal texture, however, ranges from smooth to strongly papillose and is discussed in the section on anatomy below.

The male spikelets are hyaline and early deciduous, and their relative size with respect to the female spikelets is apparently of some taxonomic value.

The caryopses of most species are ovoid-ellipsoid, and the hilum is central punctiform or short-elliptical, a type not present in other bambusoid grasses (Calderón & Soderstrom, 1980). However, in *R. esenbeckii* (but not its putative sister species *R. minima*) the hilum is short-linear.

Anatomy

A scanning electron microscope study of the mature female florets proved useful in clarifying species limits in *Raddiella*, just as in *Panicum* (Zuloaga, 1987) and *Olyra* (Soderstrom & Zuloaga, 1989). Most species of *Raddiella* had distinctive lemmatal epidermal features that are described below. Common to all species was the presence near the base and/or apex of the palea of circular excavations, 10–15 μm diam., similar to those present on the female paleas of various species of *Olyra* L. and *Parodiolyra* Soderstrom & Zuloaga (Soderstrom & Zuloaga, 1989). These excavations are apparently caused by the deflation of certain cells when placed in the vacuum of the scanning electron microscope.

Raddiella esenbeckii (Figs. 1, 2). Female lemma completely smooth.

Raddiella kaieteurana (Figs. 3, 4). Both lemma and palea covered throughout with simple papillae 4–5 μm diam.

Raddiella lunata (Figs. 9, 10). Both lemma and palea with cells with a single large, central, compound papilla 9–11 μm diam., bearing on its raised margins 3–5 smaller papillae 3–4 μm diam.

Raddiella malmeana (not illustrated). Lemma completely smooth (but available floret slightly immature).

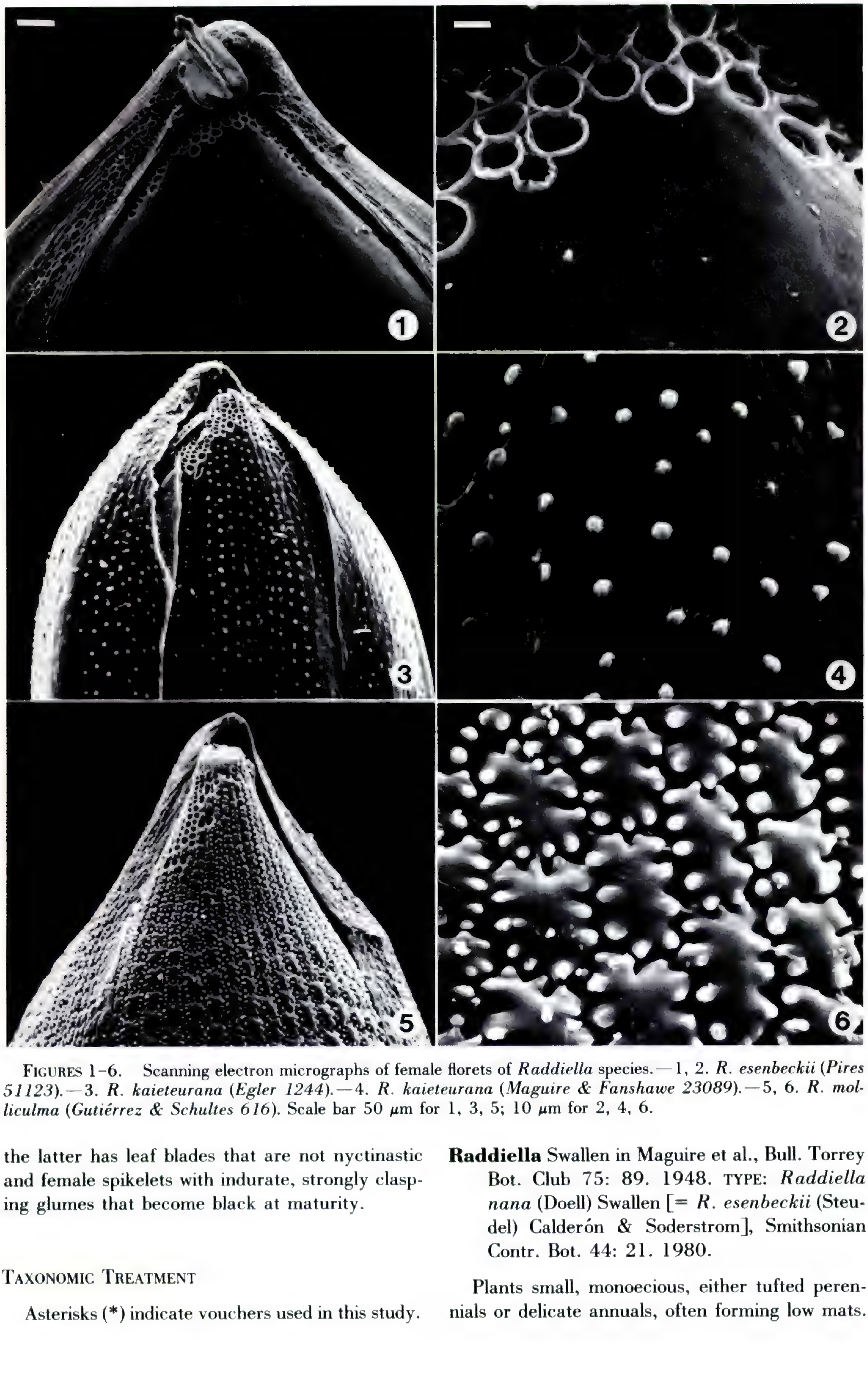
Raddiella minima. Not included in scanning electron microscope study; in an optical microscope, the lemma appears to be completely smooth, as in *R. esenbeckii*.

Raddiella molliculma (Figs. 5, 6). Both lemma and palea with the central portion of each cell enlarged and protruding (ca. 30 × 20 μm), and with 10–12 papillae, 3–5 μm diam., present along the undulating margins.

Raddiella potaroensis (Figs. 7, 8). Both lemma and palea with cells with the central portion of each cell enlarged, 15–18 μm diam., surmounted by 7–10 smaller papillae 3–4 μm diam.

Relationships

The possible affinities of *Raddiella* with several other putatively related genera of the Olyreae are summarized in Table 1. It will be noted that the type species, *R. esenbeckii*, has several characters in common with *Parodiolyra lateralis* (Nees) Soderstrom & Zuloaga rather than with the phreatophytic species of *Raddiella* (with the possible exception of the poorly known *R. minima*): perennial habit; firmly membranous leaves; smooth female florets; and a short-linear rather than punctiform hilum. Arguing for the retention of the phreatophytic species within *Raddiella* is the presence of the following feature in common between them and *R. esenbeckii*: few-flowered panicles with the sexes usually separate, the males terminal and females axillary. Moreover, *R. esenbeckii* and *P. lateralis* have quite different chromosome numbers ($n = 10$ and 18 (Davidse & Pohl, 1978), respectively), and



FIGURES 1–6. Scanning electron micrographs of female florets of *Raddiella* species.—1, 2. *R. esenbeckii* (*Pires 51123*).—3. *R. kaieteurana* (*Egler 1244*).—4. *R. kaieteurana* (*Maguire & Fanshawe 23089*).—5, 6. *R. molliculma* (*Gutiérrez & Schultes 616*). Scale bar 50 μm for 1, 3, 5; 10 μm for 2, 4, 6.

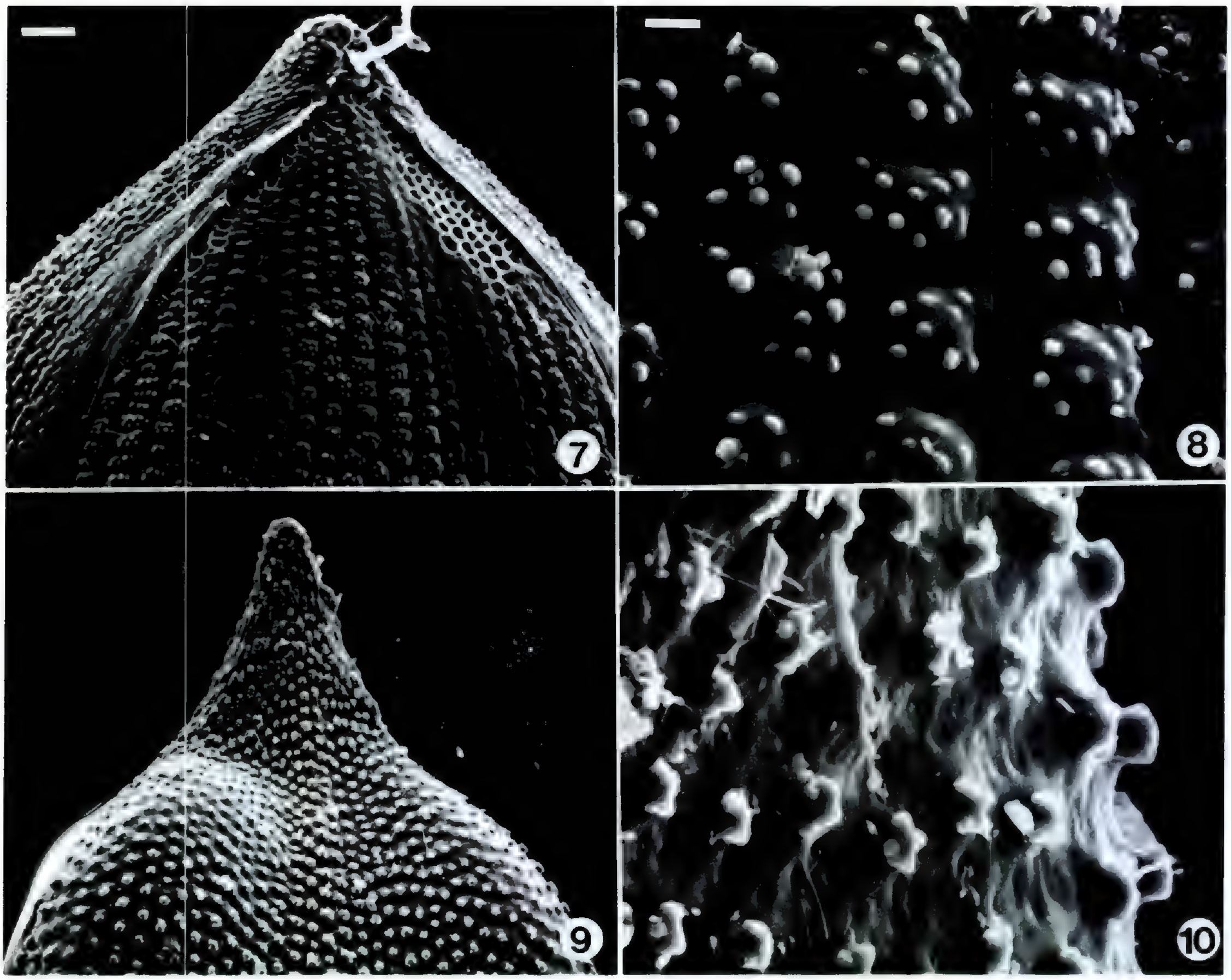
the latter has leaf blades that are not nyctinastic and female spikelets with indurate, strongly clasping glumes that become black at maturity.

TAXONOMIC TREATMENT

Asterisks (*) indicate vouchers used in this study.

Raddiella Swallen in Maguire et al., Bull. Torrey Bot. Club 75: 89. 1948. TYPE: *Raddiella nana* (Doell) Swallen [= *R. esenbeckii* (Steudel) Calderón & Soderstrom], Smithsonian Contr. Bot. 44: 21. 1980.

Plants small, monoecious, either tufted perennials or delicate annuals, often forming low mats.



FIGURES 7–10. Scanning electron micrographs of female florets of species of *Raddiella*.—7, 8. *R. potaroensis* (*Maguire & Fanshawe 32277*).—9, 10. *R. lunata* (*Rondon s.n.*). Scale bar 50 μm for 7, 9; 10 μm for 8, 10.

Leaves small, pseudopetiolate; blades elliptical to ovate-triangular, often strongly asymmetrical and with an apiculate apex, exhibiting sleep movements or not. Inflorescences small, few-flowered, 1–several from both terminal and axillary nodes, barely exserted from the leaf sheaths, 2–6(–12) spikelets per inflorescence. Terminal inflorescences male and female or more commonly strictly male, rarely strictly female; axillary inflorescences either all female or with female and male spikelets; female spikelets minutely cupulate at apices. Spikelets 1-flowered, the broad female spikelets shorter than to as long as the narrow male spikelets. Female spikelets falling entire from pedicels or in one species the glumes persistent and the floret falling, ovate-lanceolate; glumes subequal, membranous, as long as the spikelet, acute, 3–5-nerved, the lateral nerves often obscure; floret elliptical to ovoid, acute, glabrous, thinly coriaceous, stramineous or becoming dark when mature, the margins of the lemma inrolled over the edges of the palea; style 1, stigmas 2. Caryopsis ovoid to globose, brownish tan; embryo small, basal; hilum punctiform or short-linear. Male spikelets borne on filiform pedicels, hyaline, glabrous, early deciduous, linear to lanceolate; glumes absent; lemma 3-nerved; palea 2-nerved; stamens 3.

Distribution and ecology. Seven species ranging from Panama and Trinidad to Bolivia and Brazil (to São Paulo); savannas, forest margins, or among wet rocks near rivers and waterfalls, from near sea level to 1,500 m.

Raddiella has two centers of diversity: (1) the Guayana Highlands, with four species, two of them endemic (including the Colombian species *R. molliculma* at the far western edge of the Guayana Highlands formation); and (2) the western Brazilian Planalto from Rondônia to northern Mato Grosso and southern Pará, with five species including three endemics. More new species may be expected from both areas.

KEY TO THE SPECIES OF *RADDIELLA*

1a. Female florets smooth 2
  2a. Leaf blades elliptical, ± symmetrical, acute at both base and apex; female glumes de-

TABLE 1. Comparison of *Raddiella* with related genera.

	Olyra	*Parodiolyra lateralis*	*Parodiolyra* (2 species)	*Raddiella esenbeckii*	*Raddiella* (phreatophytic species)
Habit	Caespitose perennials	Caespitose to sprawling perennials	Sprawling perennials	Caespitose perennials	Sprawling annuals
Nyctinasty	−	−	−	+	−?
Leaf blade asymmetry	− (+)	+	−	+	−
Leaf blade texture	Firm	Firm	Firm	Firm	Delicate
Axillary inflorescences well developed	−	−, +	−, +	+	+
Inflorescence size	Large	Moderate	Moderate	Small	Small
Sexes in separate inflorescences	− (+)	−	−	+	+
Female spikelet pedicels clavate or filiform	c (f)	f	f	f	f
Female spikelet falling entire	− (+)	+	+	−	+
Female spikelet: thickened internode between glumes	−	+	+	+	+
Female floret texture	Variable	Smooth	Smooth, viscid	Smooth	Papillose or smooth
Hilum	Fully linear	Short-linear (1/2 to 3/4 length)	Short-linear (ca. 1/2 length)	Short-linear (ca. 1/2 length)	Punctiform
Chromosome *n*=	7, 10, 11, 20, 22	18	Unknown	10	Unknown

ciduous along with the floret ..... 4. *R. malmeana*

2b. Leaf blades ovate-triangular, asymmetrical, the base truncate, the apex acute or apiculate; female glumes persistent, only the floret deciduous 3

3a. Female spikelets 1.9–2.7 mm long; male spikelets 3–5 mm long, (1–)2–4 per inflorescence; leaf blades 9–22 mm long, 4–11 mm wide; caryopsis with the hilum short-linear; widespread ..... 1. *R. esenbeckii*

3b. Female spikelets 1–1.4 mm long; male spikelets ca. 1.3 mm long, 1 per inflorescence; leaf blades 4–6 mm long, 2.7–3.3 mm wide; caryopsis with the hilum punctiform; rare, Pará, Brazil ..... 5. *R. minima*

1b. Female florets minutely papillose with simple or compound papillae all over surface 4

4a. Female florets lunate (crescent-shaped) in profile, dorsally compressed, abruptly beaked; female floret epidermis with a single compound papilla in the middle of each cell; rare, Rondônia, Brazil ..... 3. *R. lunata*

4b. Female florets straight and lanceolate in profile, terete, not beaked; female floret epidermis without a compound papilla in the middle of each cell 5

5a. Inflorescences long-exserted, some peduncles at least 5 cm long; female florets with papillae along the cell margins; rare, Caquetá, Colombia ..... 6. *R. molliculma*

5b. Inflorescences with bases included in leaf sheaths, or short-exserted on peduncles less than 1 cm long; female florets with 1–several papillae per cell; Venezuela, Guianas, Brazil 6

6a. Leaf blades with the lower surface hispid to strigose throughout; female spikelets 1.4–2 mm long; female floret epidermis with 1 simple papilla per cell; male spikelets 4–5.8 mm long ..... 2. *R. kaieteurana*

6b. Leaf blades with the lower surface glabrous or with short, scabrid hairs only on the veins; female spikelets 1.3–2.3 mm long; female floret epidermis with 7–10 simple papillae per cell; male spikelets 2.7–4.2 mm long ..... 7. *R. potaroensis*

1. **Raddiella esenbeckii** (Steudel) Calderón & Soderstrom, Smithsonian Contr. Bot. 44: 21. 1980. *Panicum esenbeckii* Steudel, Syn. Pl. Glumac. 1: 90. 1854; based on *Panicum laterale* var. *β* Nees, Agrost. Brasil. 213. 1829. Basis in part of *Olyra nana* Doell in C. Martius, Fl. Bras. 2(2): 329. 1877, nom. superfl. *Raddia nana* (Doell) Chase, Proc. Biol. Soc. Wash. 21: 185. 1908. *Raddiella nana* (Doell) Swallen, Bull. Torrey Bot. Club 75: 89. 1948. TYPE: Brazil. Amazonas: Rio Negro, Ega, *Martius s.n.* (holotype, M? not seen; the same specimen designated as a lectotype of *O. nana* M?, not seen). Figures 1, 2, 13A–D.

Densely tufted perennials, with up to 60 unbranched culms per clump. Culms sprawling, decumbent to geniculate, the erect portions 8–40 cm tall, wiry; internodes cylindrical, glabrous to sparsely pilose with short, retrorse hairs; nodes thickened, densely pilose with whitish retrorse hairs. Leaves in complements of 7–15, nyctinastic, the blades folding upwards at night or under water stress; sheaths striate, glabrous to short-pilose, densely so toward the summit, one margin membranous, the other short-ciliate, short-auricled, the auricle membranous on one side; ligules ca. 0.3 mm long, membranous, apically short-ciliate; pseudopetioles ca. 0.5 cm long, densely pilose; blades 9–22 mm long, 4–11 mm wide, ovate-triangular, asymmetrical, truncate at the base, acute and short-apiculate at the apex, flat, firmly membranous, either glabrous, or short-pilose near the base on the upper surface, to densely puberulent on both surfaces, the lower margins ciliate, the lower surface purplish in some specimens. Inflorescences terminal and axillary; terminal inflorescences 3–5, with male spikelets only, on cylindrical, glabrous peduncles 1–2 cm long, each inflorescence with (1–)2–4 male spikelets on short, glabrous pedicels; axillary inflorescences both female and male, the female inflorescences on short-pilose peduncles 5–8 mm long, each bearing 2 short-pedicelled female spikelets. Female spikelets 1.9–2.7 mm long, 0.7–0.9 mm wide, ovoid; glumes firmly membranous, greenish becoming blackish, sparsely to densely short-pilose with spreading hairs, 3-nerved, persistent, the internode between the glumes thickened, the lower glume acute, slightly shorter than the acuminate upper glume; floret 1.6–2 mm long, ellipsoid, coriaceous, smooth, shiny, glabrous, whitish becoming dark, deciduous. Caryopsis 1–1.2 mm long, 0.7–0.8 mm wide, long-ellipsoid, dorsally compressed; hilum short-linear, ca. ⅓ the length of the caryopsis, extending from near the center to near the base; embryo ca. ⅙ the length of the caryopsis. Male spikelets borne on minutely cupuliform pedicels, 3–5 mm long, ca. 1 mm wide, lanceolate, acuminate, greenish to purplish, hyaline, glabrous to sparsely hispid with short hairs; glumes occasionally present, to 3.7 mm long, linear-lanceolate, sparsely hispid; lemma as long as spikelet, lanceolate, acuminate, glabrous to sparsely hispid with short hairs; stamens with anthers 1.3–3 mm long.

Distribution and ecology. Panama and northern South America (including Trinidad) to Bolivia and central Brazil (Fig. 11); from 0 to 1,500 m in semishaded or more often dryish, open places: gallery forests, woodlands, savannas, and cerrados, often on rocky or sandy soil.

Chromosome number. $n = 10$ (Davidse & Pohl, 1972).

Representative specimens examined. PANAMA. PANAMA: 7 mi. N of Cerro Azul, 2,600 ft., 13 Nov. 1965, *Blum et al. 1789* (MO); Cerro Campana, 900 m, 21 Jan. 1984, *van der Werff & Herrera 6156* (MO); hills NE of Hacienda La Joya, 50–300 m, 9 Dec. 1934, *Dodge et al. 16882* (MO). HERRERA: N slope of Cerro Alto Higo, 2,400 ft., 5 Aug. 1978, *Hammel 4202* (MO). COLOMBIA. AMAZONAS: Bella Vista, Río Igará–Paraná, 8 Sep. 1973, *Sastre 2152* (US). META: La Macarena, Río Guayabero, Sabanas de Arenisca, Jan.–Mar. 1959, *García-Barriga & Jaramillo 17089* (US). VAUPÉS: Río Guainía, Caño del Caribe, between Isla del Venado and San José, 2°45′N, 67°50′W, 2 Nov. 1952, *Schultes et al. 18262* (US); Río Guainía basin, Río Naquieni, vicinity of Cerro Monachí, June 1948, *Schultes & López 10115* (US); Río Kananarí, Cerro Isibukuri, 28 Oct. 1951, *Schultes & Cabrera 14452* (US). VENEZUELA. AMAZONAS: Piedra Arauicaua, Río Yatua, 27 Sep. 1957, *Maguire et al. 41608* (US), 15 July 1959, *Wurdack & Adderley 43457* (US); Río Cunucunuma, occasional on moss-covered boulders, upriver from Playa Alto, 14 Nov. 1950, *Maguire et al. 29500* (US); banks of Río Cuao, above Cuao Creek, 25 Nov. 1948, *Maguire & Politi 27376* (US); Río Atacavi, ca. 1 km above the confluence with Río Atabapo, 6–19 July 1969, *Bunting et al. 3658* (US); Cerro Duida, Río Cunucunuma, Culebra Creek, 1,500–1,600 m, 21 Nov. 1950, *Maguire et al. 29629* (US). ANZOÁTEGUI: Fila El Purgatorio, S of El Zamuro, 10°02′N, 64°17′W, 1,100 m, 24 Nov. 1981, *Davidse & González 19335* (MO). BOLÍVAR: cercanías del campamento en el lado sur del Río Ichún, tributario del Río Paragua, debajo del Salto María Espuma, 4°46′N, 63°18′W, 30 Dec. 1961, *Steyermark 90470* (US); Dist. Heres, San Salvador de Paúl, 6°02′N, 62°53′W, 2 Dec. 1982, *Davidse & Huber 23128* (US). SUCRE: 8 km S de Santa Fé, 10°16′N, 64°24′W, 230 m, *Davidse & González 19069* (MO, US); carretera Guanta–Los Altos, *Tamayo 2146* (US). TÁCHIRA: Dist. Uribante, Siberia to Pregonero, 8°55′N, 71°40′W, 1,300 m, 11 July 1983, *van der Werff & González 5365* (MO). TRINIDAD. Aripo Savanna along the Cumuto road, 3 Nov. 1929, *Broadway 7685* (MO), 5 Aug. 1970, *Davidse 2550* (MO, US). GUYANA. Kaieteur savanna, 5 Sep. 1937, *Sandwith 1375* (US), 11 Feb. 1962, *Cowan & Soderstrom 1807* (US); Waranama ranch, *Harrison & Persaud 1069* (BRG, K); Lama Dam, *Jenman 5971* (BRG).

FIGURE 11. Distribution of *Raddiella esenbeckii*.

SURINAM. Brinckhill Nature Reserve, 14 Dec. 1967, *Wildschut & Teunissen 11346* (US); Moengo tapoe ad Grote Zwiebelzwamp, *Lanjouw & Lindeman 872* (NY, U); Sipaliwini savanna, *Oldenburger et al. 141* (U). FRENCH GUIANA. Passoura, 3 Apr. 1958, *Hoock 942* (CAY); Savane des Singes, 5°05′N, 52°42′W, *Cremers & Hoff 10680* (CAY, US). BRAZIL. AMAPÁ: Matapí, *Pires & Silva 4797* (US); Igarapé do Paia, km 110 on road to Amapá, 20 July 1962, *Pires & Cavalcante 52233* (MO, NY, US). AMAZONAS: 3 km E of Borba near the Rio Madeira, 4°23′S, 59°35′W, 22 June 1983, *Hill 12753* (F, MO, US); Rio Jauarí, affluent of Rio Aracá, 0°49′N, 63°20′W, July 1985, *Huber et al. 10710* (MO); Rio Urubú, Serra da Lua, 6 June 1968, *Prance et al. 5005* (MO); Manaus, Rio Cuieiras, Igarapé Cachoeira, 19 Dec. 1961, *Rodrigues & Wilson 3191* (US); km 38 on road from Humaitá to Pôrto Velho, 6 May 1982, *Teixeira et al. 260* (MO). BAHIA: Serra do Sincorá, 16 km N of Barra da Estiva on the Paraguaçú road, 13°20′S, 41°20′W, 31 Jan. 1974, *Harley et al. 15746* (US); 2–5 km N of Lençois, 11 June 1981, *Mori & Boom 14339* (MO). DISTRITO FEDERAL: Bacia do Rio Bartolomeu, 5 May 1980, *Heringer et al. 4626* (US); Chapada da Contagem, Parque Municipal do Gama, ca. 25 km W of Brasília, 1,100 m, 3 Feb. 1968, *Irwin et al. 19474* (US); 700–1,000 m, 31 Aug. 1964, *Irwin & Soderstrom 5801* (US). GOIÁS: ca. 10 km S of Alto do Paraíso, 22 Mar. 1969, *Irwin et al. 24921* (MO, US); S Serra Dourada, gallery forest 20 km E of Formosa, 13°45′S, 48°50′W, 18 May 1956, *Dawson 14956* (US); vicinity of Goiabeira, between Anápolis and Goiás, 23 Mar. 1930, *Chase 11510* (MO, US); ca. 3 km E of Alto Paraíso on road to Nova Roma, 7

Mar. 1973, *Anderson 6604* (MO, US). MARANHÃO: Pedra Caida, 35 km N of Carolina, 7°08′S, 47°25′W, 14 Apr. 1983, *Taylor et al. E-1240* (US). MATO GROSSO: ca. 5 km N of Barra do Garças, S face of mountain, 7 May 1973, *Anderson 9885* (US); km 762, Santarém-Cuiabá road, 9°35′S, 54°55′W, *Amaral et al. 806* (F, MO). MINAS GERAIS: Vaccaria, Serra do Cipó, Apr. 1925, *Chase 9257* (MO, US); Metallurgica, Serra de Ouro Branco, 23 Dec. 1929, *Chase 10290* (MO, US); Rio Jequití, ca. 25 km E of Diamantina, 790 m, 21 Mar. 1970, *Irwin et al. 27993* (MO, US); Serra do Espinhaço, 3.5 km by road SW of Rio Jequití and Mendanha, 14 Apr. 1973, *Anderson 8922* (US). PARÁ: 7 km SE of Vigía, 0°55′S, 48°04′W, 31 Mar. 1980, *Davidse et al. 17689* (MO); Rio Aruá, *Black 49-844* (US). RONDÔNIA: Abunã, Rio Madeira, 11 July 1968, *Prance et al. 5887* (MO); Pôrto Velho, caminho para o km 8, 26 May 1952, *Black & Cordeiro 52-14526* (US). SÃO PAULO: São José dos Campos, 16 Dec. 1909, *Löfgren 4680* (US). BOLIVIA. BENI: Prov. Vaca Diez, 15 km W de Guayamerim, camino a Riberalta, en campos con rocas aflorantes, 17 Apr. 1979, *Krapovickas & Schinini 35062* (US).

This species is variable in stature. Alone among members of the genus, the leaf blades exhibit sleep movements, folding upwards at night or under water stress.

The superficially similar *Parodiolyra lateralis* differs in its sprawling habit, larger, more rigid blades lacking sleep movements, and larger, more open mixed panicles with mature female spikelets with blackish, indurate, 3–7-nerved glumes that strongly invest the floret.

2. Raddiella kaieteurana Soderstrom, Mem. New York Bot. Gard. 12(3): 6. 1965. TYPE. Guyana: Kaieteur Plateau, on moist cliff faces along trail from Kaieteur Plateau to Tukeit, 1,100 ft., 4 Feb. 1962, *R.S. Cowan & T.R. Soderstrom 1742*. (holotype, US*; isotypes, GH, K, NY, P). Figures 3, 4, 13E–G.

Delicate mat-forming herbs of indefinite duration. Culms weak, decumbent, rooting and branching at the lower nodes, the flowering portion 5(–20) cm long, many-noded; internodes compressed, glabrous. Leaves with the sheaths striate, longer than the internodes, greenish to purplish, with long hairs near the apex, otherwise sparsely pilose to glabrescent; ligules membranous, 0.3–0.5 mm long; pseudopetioles 0.5 mm long, hirtellous; blades 8–17 mm long, 3–8 mm wide, flat, delicately membranous, densely hispid to strigose on both surfaces with long and short hairs, the base slightly asymmetrical, obtuse, and subcordate, the apex acute and slightly apiculate, the margins ciliate throughout or only toward the base of the blade. Inflorescences terminal and axillary from the upper nodes, with bases included in leaf sheaths or short-exserted on peduncles less than 1 cm long; terminal inflorescences 2–6, mostly male, each bearing 1–2 spikelets, or occasionally female spikelets present; axillary inflorescences female, exserted up to 3 mm on filiform peduncles and bearing 1–3 female spikelets on divergent pedicels 1.5–5 mm long. Female spikelets 1.4–2 mm long, 0.6–0.8 mm wide, ellipsoid, falling entire; glumes ovate-elliptical, acuminate, subequal, prominently nerved, sparsely short-pilose with spreading hairs to uncommonly glabrous, greenish, the lower glume 3-nerved, separated from the 3–5-nerved upper glume by a short internode; floret 0.8–1.7 mm long, 0.5–0.6 mm wide, narrowly ellipsoid, dorsally compressed, minutely papillose, whitish becoming brownish at maturity; lemma evidently 3–5-nerved. Caryopsis 0.6–0.8 mm long, 0.4–0.7 mm wide, broadly ellipsoid; hilum oblong, placed in the middle of the caryopsis and extending slightly toward the base; embryo ⅛ or less the length of the caryopsis. Male spikelets borne on pedicels 0.5–2.3 mm long, 4–5.8 mm long, 0.6–0.8 mm wide, fusiform, hyaline, sparsely short-pilose toward the apex; glumes occasionally present, to 4 mm long, linear-lanceolate; lemma 3–5-nerved; stamens with anthers 2–2.8 mm long.

Distribution and ecology. Venezuela (Bolívar), Guyana, Surinam, and northern Brazil (Pará); on damp cliff faces or in the spray of waterfalls, from 100 to 810 m (Fig. 12).

Additional specimens examined. VENEZUELA. BOLÍVAR: Dist. Piar, Amaruay-tepui, S side about 1 km from SW corner of tepui, 5°54′N, 62°15′W, 550–810 m, 26 Apr. 1986, *Liesner & Holst 20369* (MO). GUYANA: semishaded rock face in forest along trail from Kaieteur Falls to Tukeit, about 1 km E of the airstrip, 300 m, *Cowan & Soderstrom 2027* (K, NY, US); 29 Apr. 1944, *Maguire & Fanshawe 23087* (MO, NA, NY, US*); 24 Feb. 1962, *Cowan & Soderstrom 1918* (US); Apr. 1988, *Hahn et al. 4163* (BRG, US); anno 1881, *Jenman 1277* (US). SURINAM.: Tafelberg, base of N escarpment, under drips, 390 m, 11 Aug. 1944, *Maguire 24327* (MO, NA, NY, U); NW side, *Geyskes 998* (U). BRAZIL. PARÁ: Rio Cururú (affluent of Rio Tapajos), Cachoeira Kereputiá, in a hole on sandstone rocks, 3 Mar. 1960, *Egler 1244* (US*).

As presently conceived, this species is variable. In *Egler 1244* the female spikelets are only 0.9–1 mm long and the glumes are covered with short hairs, but scanning electron micrographs revealed that female floret texture is similar to that of typical *R. kaieteurana*. An unusual feature of *Cowan & Soderstrom 1918* is the presence of terminal female inflorescences with two spikelets. *Liesner & Holst 20369* differs from typical *R. kaieteurana* in its short-pilose to glabrous leaf blades and completely glabrous female glumes.

FIGURE 12. Distribution of *Raddiella kaieteurana*, *R. lunata*, *R. malmeana*, *R. minima*, *R. molliculma*, and *R. potaroensis*.

3. Raddiella lunata Zuloaga & Judziewicz, sp. nov. TYPE. Brazil. Rondônia: Serra dos Pacáas Novos, Cab. do Cautário, planta umbrophila, na entrada das lapas, firmas, predas, etc., Mar. 1917, *C. Rondôn s.n.* [as *J.G. Kuhlmann 1863*] (holotype, RB; isotypes, K, MO, NY, SI, SP, US*). Figures 9, 10, 14.

Ab omnibus conspecificis differt: spicula, flosculo et caryopside lunatis abrupte rostratis, necnon flosculo papilla composita in medio cuiusque cellulae praedito.

Delicate, sprawling, mat-forming annuals. Culms decumbent, rooting and branching at the lower nodes, the erect portions 7–15 cm tall, many-noded, unbranched; internodes cylindrical, hollow, glabrous; nodes thickened, with short, retrorse, whitish hairs. Leaves with the sheaths striate, glabrous, slightly inflated, the margins membranous, the auricles membranous, glabrous, the summit truncate; ligules not noted; pseudopetioles ca. 0.1 mm long, brownish, short-pilose; blades 10–15 mm long, 2.5–3.5 mm wide, lanceolate, delicately

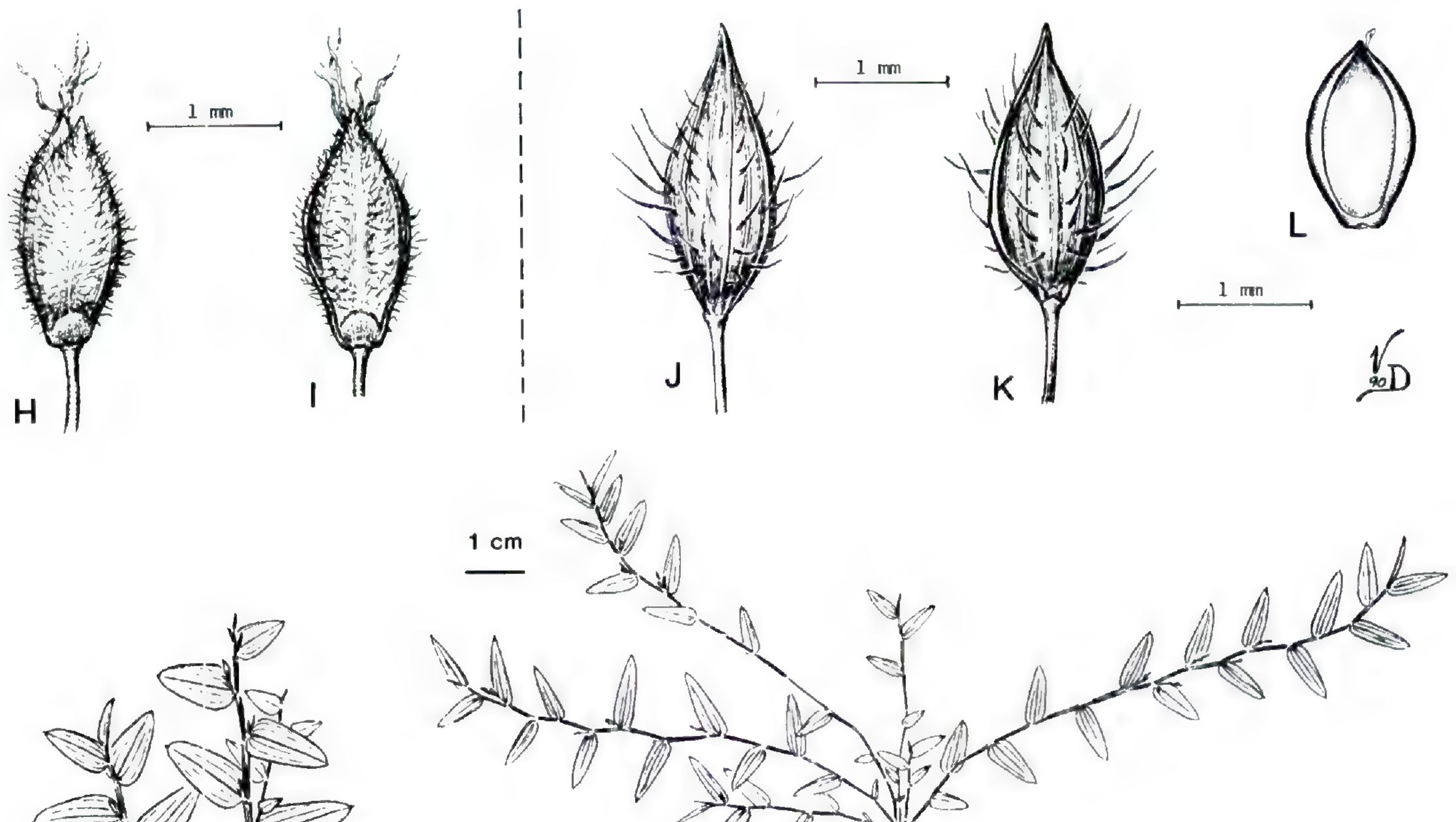


FIGURE 13. A–D. *Raddiella esenbeckii* (*Huber 2126*).—A. Habit.—B. Female spikelet.—C. Female floret.—D. Male spikelet. E–G. *Raddiella kaieteurana* (*Liesner 20414*).—E. Habit.—F. Female spikelet.—G. Female floret. H, I. *Raddiella molliculma* (*Grassl 10024*).—H. Female spikelet, dorsal view.—I. Female spikelet, ventral view. J–L. *Raddiella potaroensis* (*Cowan & Soderstrom 2162*).—J. Female spikelet, dorsal view.—K. Female spikelet, ventral view.—L. Female floret.

membranous, glabrous to sparingly short-pilose on both surfaces (especially on the veins below), the base slightly asymmetrical, acute at the apex, the margins scabrous. Inflorescences both terminal and axillary, with 1–several inflorescences produced at each node, short-exserted on glabrous, filiform peduncles up to 10 mm long; individual inflorescence a contracted, racemelike panicle 5–10 mm long, the rachis slightly sinuous, glabrous, alternately bearing 2–12 spikelets on short pedicels 0.5–1.5 mm long, or occasionally with a lower branch up to 3 mm long bearing 2 spikelets; terminal spikelet female, the lateral ones male or occasionally a few females. Female spikelets ca. 1 mm long, obovoid, lunate in profile, falling entire; glumes delicately membranous, short-hispid, 3-nerved, the lower glume not covering the apex of the floret, the upper glume as long as the floret, flat; floret 0.8–1 mm long, 0.5–0.6 mm wide, obovoid, dorsally compressed, concave on the ventral side, convex on the dorsal side, acute at the base, rather abruptly beaked at the apex, coriaceous, whitish becoming brown at maturity, strongly papillate; lemma conspicuously grooved on the dorsal surface, slightly winged, the margins covering the edges of the palea with wide margins. Caryopsis 0.6–0.8 mm long, 0.5–0.6 mm wide, ovoid, lunate, of the same general morphology as the floret, slightly winged; hilum

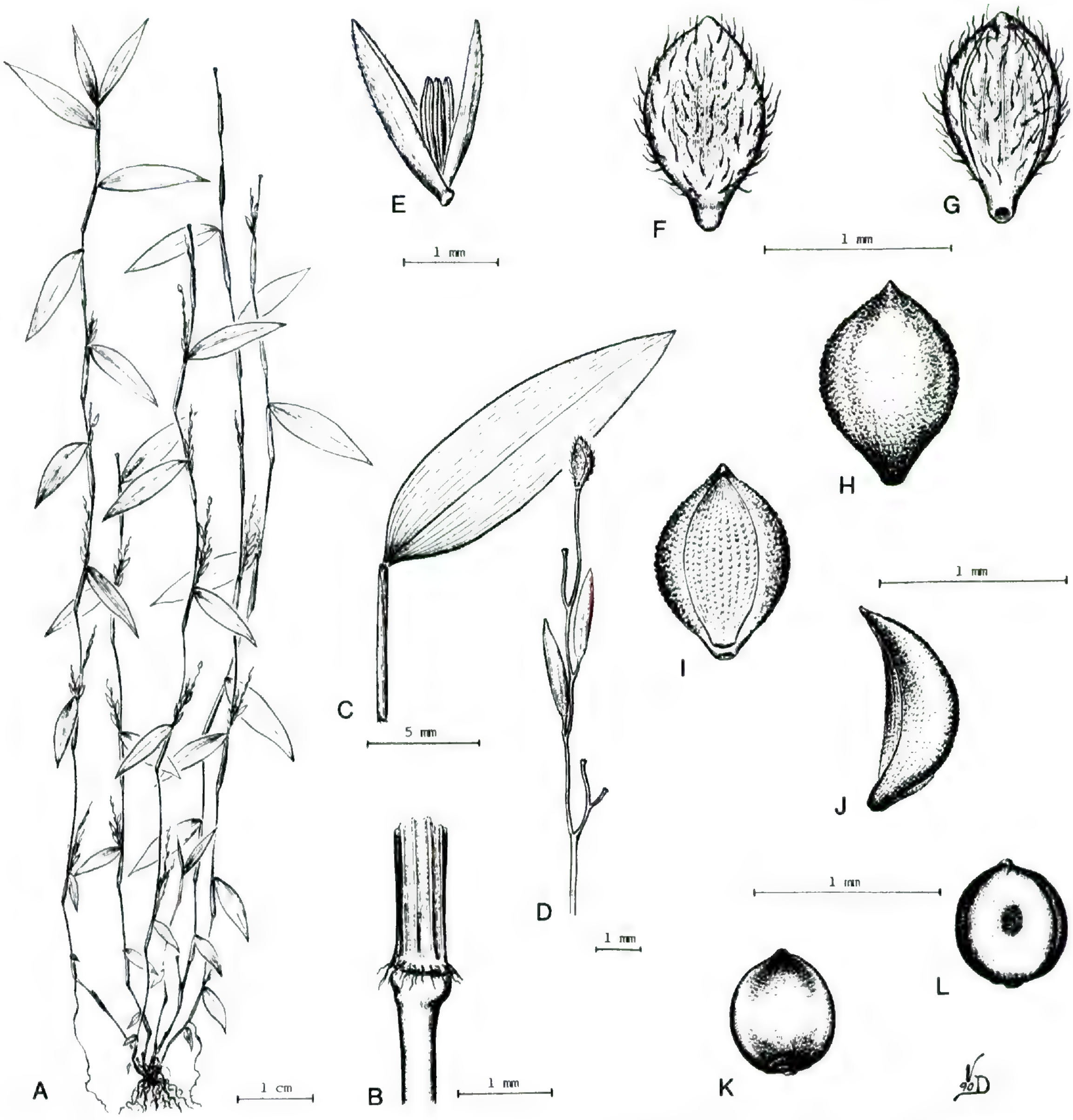


FIGURE 14. *Raddiella lunata* (*Rondon s.n.*).—A. Habit.—B. Detail of a node.—C. Leaf.—D. Inflorescence.—E. Male spikelet. F–J. Female spikelet.—F. Lower glume.—G. Upper glume. H–J. Floret.—H. Dorsal view.—I. Ventral view.—J. Lateral view. K, L. Caryopsis.—K. Dorsal view.—L. Ventral view.

rounded at the middle portion of the caryopsis; embryo ½ the length of the caryopsis. Male spikelets 1.7–2.7 mm long, lanceolate-elliptical, acute, hyaline, glabrous; lemma 3-nerved; stamen with anthers 1–1.5 mm long.

Distribution and ecology. Known only from the type collection made in the Serra dos Pacáas Novos in Rondônia, Brazil (Fig. 12).

This species differs from all other congeners in its lunate (crescent-shaped, hence the specific epithet) female floret that tapers rather abruptly to both ends, and the surface of the floret, which has a single compound papilla on each cell. The form of the female spikelets could be associated with dispersion by water.

In the mature plants at hand, the culms disarticulate readily at the nodes. Whether this represents an adaptation for dispersal or is merely indicative of senescence is unclear.

4. **Raddiella malmeana** (E. Ekman) Swallen, Bull. Torrey Bot. Club 75: 89. 1948. *Olyra malmeana* E. Ekman, Ark. Bot. 10(17): 21. 1911. *Raddia malmeana* (E. Ekman) A.

Hitchc., Contr. U.S. Natl. Herb. 22: 505. 1922. TYPE. Brazil. Mato Grosso: Santa Ana da Chapada, Buriti, in proruptis rupis ad cataractam junta cum Sphagni, 16 June 1894, *Malme (Regnell Expedition I) 1684* (holotype, S n.v.; isotype, US*).

Annuals. Culms decumbent and rooting at the lower nodes, the erect portions to 20 cm tall (according to original description), many-noded, unbranched; internodes glabrous. Leaves with the sheaths longer than the internodes, striate, glabrous, the margins membranous, the auricles membranous; ligules ca. 0.3 mm long, membranous; pseudopetioles ca. 0.5 mm long, narrow, brownish, glabrous; blades 5–10 mm long, 2–4 mm wide, elliptical, delicately membranous, flat, sparingly short-pilose on both surfaces or with scabrid hairs on the veins only on the lower surface, ± symmetrical, acute at both base and apex, the margins scaberulous. Inflorescences terminal and axillary from the uppermost nodes, partially included in the sheaths; terminal inflorescences bearing male spikelets only; axillary inflorescences bearing female spikelets, congested, few-flowered, the axis and pedicels smooth, glabrous, to 2 mm long. Female spikelets 1.8–2.1 mm long, 0.5–0.6 mm wide, narrowly ovoid, falling entire; glumes acuminate, short-hispid with long, thickened hairs mainly on the nerves, the lower glume 3-nerved, the upper glume 3–5-nerved; floret ca. 1.5 mm long, narrowly ovoid (but none fully mature), whitish, smooth, shiny. Caryopsis not seen. Male spikelets 1.7–2 mm long, ca. 0.4 mm wide, lanceolate, hyaline, glabrous, shiny; lemma 3-nerved; stamens with anthers ca. 1 mm long.

Distribution and ecology. Endemic to wet rocks near streams at low elevations in Mato Grosso and Pará, Brazil (Fig. 12).

Additional specimens examined. BRAZIL. MATO GROSSO: Utiarity, Rio Papagaio, margin of waterfall, May 1918, *Kuhlmann 1866* (US). PARÁ: estrada Santarém–Cuiabá, 877 km de Cuiabá, vale de solo pedregoso, embaixo da Cachoeira da Luz do Rio Curuá, 8°45′S, 54°57′W, 350 m, 2 May 1983, *Silva 196* (MO).

This species is related to *R. potaroensis* and *R. kaieteurana*, but differs in its smooth female florets, and in female and male spikelets of similar size.

5. Raddiella minima Judziewicz & Zuloaga, sp. nov. TYPE. Brazil. Pará: Município de Itaituba, km 771 estrada Santarém–Cuiabá, próximo a divisão Pará–Mato Grosso, mata de cerrado solo pedregoso, vegetação rupestre, 9°35′S, 54°35′W, 22 Apr. 1983, *I.L. Amaral, N. Silva, O.P. Monteiro, J. Lima, L. Brako, W.D. Reese & M. Dibben 883* (holotype, INPA; isotypes, MO, NY).

A *Raddiella esenbeckii* differt lamina minore (4–6 × 2.7–3.3 mm) et spiculis mascula et femina minoribus (1–1.3 mm longis), caryopside hilo punctiformi centrali praedita.

Tiny, straggling herbs of indefinite duration. Culms to 6 cm long, filiform, geniculate, multibranched, internodes purple, glabrous; nodes with a few very short retrorse hairs. Leaves in loose complements of 3–5; sheaths shorter than the internodes, usually shorter than the blades, glabrous to short-pilose, 5-nerved, slightly inflated, the upper margins ciliate, abruptly truncate at the short-ciliate summit; ligule membranous, ca. 0.2 mm long; pseudopetiole 0.1–0.2 mm long, glabrous to short-pilose; blades 4–6 mm long, 2.7–3.3 mm wide, ovate-triangular, asymmetrical, glabrous, the base truncate, the apex acute and apiculate, the margins scaberulous, the abaxial surface occasionally purplish. Inflorescences terminal and axillary, terminal inflorescences 2–6, ca. 10 mm long, filiform, each terminated by a single male spikelet; axillary inflorescences 1 per each axil, ca. 3 mm long, partly included in the leaf sheath, each of 2(–3) female spikelets on short, filiform pedicels. Female spikelets 1–1.4 mm long; glumes lanceolate-ovate, acuminate, 3-nerved, glabrous to short-hispid, persistent; floret 0.9–1.2 mm long, ovoid, acute, dorsally compressed, smooth, shiny, white becoming dark, deciduous; lemma 3-nerved. Caryopsis 0.7 mm long, 0.6 mm wide, ovoid-globose; hilum punctiform, central; embryo small, basal. Male spikelets ca. 1.3 mm long, the lemma soon deciduous, elliptical, hyaline, glabrous; anthers ca. 0.6 mm long.

Distribution and ecology. Known only from the type collection, made in campo rupestre near the borders of the states of Mato Grosso and Pará, Brazil (Fig. 12).

Raddiella minima is related to *R. esenbeckii*, but differs in its conspicuously smaller leaf blades and male and female spikelets; caryopsis with punctiform, central hilum; and solitary male spikelet per inflorescence. It is not certain whether the leaves exhibit sleep movements as in *R. esenbeckii*.

Along with the Cuban endemic *Mniochloa pulchella* (Griseb.) Chase, this species is one of the world's smallest bambusoid grasses, hence its specific epithet.

6. Raddiella molliculma (Swallen) Calderón & Soderstrom, Smithsonian Contr. Bot. 44: 22. 1980. *Panicum molliculmum* Swallen in R. Schultes, Bot. Mus. Leafl. 16: 57. 1953. TYPE: Colombia. Caquetá (as "Vaupés"): Cerro de El Castillo, Río Apaporis, moist, shaded sandstone ledge with mosses and *Selaginella* spp., 16 Jan. 1942, *Gutiérrez & Schultes 616* (holotype, US*; isotype, COL). Figures 5, 6, 13H, I.

Delicate annuals. Culms decumbent, sprawling, geniculate, the erect portions 5–10 cm tall, many-noded, unbranched; internodes glabrous; nodes compressed, short-pilose with retrorse hairs. Leaves puberulent throughout with spreading, short-pilose hairs; sheaths striate, shorter than the internodes, the upper margins short-ciliate, the summit pilose; ligules membranous-ciliate; pseudopetioles ca. 0.6 mm long, brownish, short-pilose; blades 7–12 mm long, 3–4.5 mm wide, ovate-lanceolate, flat, delicately membranous, slightly asymmetrical, the base truncate, the apex acuminate, the margins scaberulous. Inflorescences terminal and axillary, abundantly produced from the uppermost nodes (6–15 from the terminal node), long-exserted on glabrous, filiform peduncles 5 cm long; individual inflorescences 2–5 mm long, few-flowered, with 1–2 terminal, short-pedicelled male spikelets and 1–2 subterminal female spikelets or occasionally with 1 or more male spikelets below; pedicels up to 1 mm long, glabrous. Female spikelets 1.3–1.5 mm long, 0.6–0.7 mm wide, narrowly ellipsoid, falling entire at maturity; glumes lanceolate-ovate, acuminate, subequal, greenish, short-hirsute, 3-nerved, the lateral nerves inconspicuous; floret ca. 1.3 mm long, 0.6–0.7 mm wide, ellipsoid, whitish, shiny, papillose. Caryopsis 0.8 mm long, 0.6 mm wide, ellipsoid, brownish; hilum oblong in the middle portion of the caryopsis; embryo small, basal. Male spikelets 1.3–2.2 mm long, 0.5–0.6 mm wide, narrowly elliptical, acuminate, hyaline, short-hispid; lemma 3-nerved; stamens with anthers 0.9–1.3 mm long, purple.

Distribution and ecology. Restricted to the Cerro de El Castillo in Caquetá, Colombia (Fig. 12), at elevations of 240–300 m on moist, shaded, sandstone cliffs.

Additional specimens examined. COLOMBIA. CAQUETÁ: Upper Río Apaporis basin, Cerro de El Castillo, 27 July 1943, *Schultes 5668a* (US), *Grassl 10024* (US).

7. Raddiella potaroensis Soderstrom, Mem. New York Bot. Gard. 12(3): 6. 1965. TYPE. Guyana. Kaieteur Plateau, bottom of Potaro Gorge near Kaieteur Falls to W rim of splash-basin of Falls, 700 ft., 13 Mar. 1962, *R. S. Cowan & T. R. Soderstrom 2162* (holotype, US*; isotypes, K, NY). Figures 7, 8, 13J–L.

Raddiella maipuriensis Soderstrom, Mem. New York Bot. Gard. 12(3): 7. 1965. TYPE: Guyana. Imbaimadai Savannas, Upper Mazaruni River, abundant in spray of Maipuri Falls, Karaurieng River, 1,250 m, 25 Oct. 1951, *B. Maguire & D. B. Fanshawe 32277* (holotype, US*; isotypes, NY, U).

Annuals. Culms weak, decumbent, branching and rooting at the lower nodes, the flowering portions 5–20 cm tall; internodes cylindrical, glabrous; nodes thickened. Leaves with the sheaths longer than the internodes, striate, glabrous, the margins membranous, the apex somewhat truncate, one side of the summit forming an auricle; ligules 0.2–0.4 mm long, membranous; pseudopetioles ca. 0.5 mm long, glabrous; blades 9–17 mm long, 3–7 mm wide, elliptical, flat, glabrous or with short, scabrid hairs only on the veins, slightly acute and asymmetrical at both ends. Inflorescences mainly axillary (one terminal inflorescence in the type of *R. maipuriensis*), 2–4 produced from each node, with the bases included in the leaf sheaths or short-exserted on peduncles less than 1 cm long, 2–3 spikelets per inflorescence, either all female or the terminal female and 1–2 male spikelets below; pedicels of male and female spikelets 1–3 mm long, filiform, glabrous. Female spikelets 1.3–2.3 mm long, ellipsoid to ovoid; glumes subequal, acute to acuminate, sparsely hispid with spreading, straggling hairs, weakly to strongly 3–5(–7)-nerved; floret 1–1.3 mm long, 0.7–0.8 mm wide, ellipsoid, acute, firmly coriaceous, shiny, whitish becoming olivaceous at maturity, papillose; lemma 3-nerved. Caryopsis ca. 0.9 mm long, 0.7 mm wide, slightly obovoid; hilum punctiform in the middle portion of the caryopsis; embryo ca. ¼ the length of the caryopsis. Male spikelets 2.7–4.2 mm long, 0.6–0.7 mm wide, lanceolate, glabrous; lemma 3-nerved; stamens with anthers 1.7–2 mm long.

Distribution and ecology. Apparently endemic to the Pakaraima Plateau of western Guyana and adjacent Bolívar, Venezuela (two sterile collections); on wet rocks near and in the spray zone of waterfalls, from 200–1,250 m (Fig. 12).

Additional specimens examined. VENEZUELA. BOLÍVAR: Sierra de Lema, in tufts at base of uppermost waterfall of headwaters of Río Chicanán at base of high sandstone NE-facing bluffs, headwaters of Río Chicanán, 80 km SW of El Dorado, *Steyermark 89568* (US); La

Gran Sabana, S of El Dorado along road to Santa Elena, ca. km 202, Salto Camá, 1,000 m, *Davidse 4872* (MO). GUYANA. Kaieteur Falls, spray zone below falls, Apr. 1988, *Hahn et al. 4635* (BRG, US).

Judziewicz (1991) did not find enough differences between *R. maipuriensis* and *R. potaroensis* to separate them as species and therefore placed the first name in the synonymy of the latter. It may be noted that the surfaces of the female florets of both taxa are identical under the scanning electron microscope. The type specimen of *R. maipuriensis* is larger than the rest of the material studied of this species, with culms ca. 20 cm tall, leaf blades 2 cm long and 0.7 cm wide, and female spikelets 1.8–2.3 mm long with acuminate, strongly nerved glumes. Two sterile Venezuelan collections, *Davidse et al. 4872* and *Steyermark 89568*, are tentatively referred to this species based on their nearly glabrous leaf blades.

EXCLUDED SPECIES

Raddiella truncata Swallen, Bull. Torrey Bot. Club 75: 89. 1948 [= *Parodiolyra lateralis* (Nees) Soderstrom & Zuloaga)].

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SYSTEMATICS AND CHROMOSOME CYTOLOGY OF *ELEUTHERINE* HERBERT (IRIDACEAE)[1]

Peter Goldblatt[2]
and Neil Snow[3]

ABSTRACT

The New World genus *Eleutherine* (Iridaceae, tribe Tigridieae) is treated as comprising two species that are characterized by a bulbous rootstock, a large subapical cauline leaf, and small, white, stellate, evening-blooming flowers. The more common *E. bulbosa* (syn. *E. plicata*) extends across South America from Bolivia and southeastern Brazil to the West Indies and is widely cultivated for its medicinal properties. Less well known is *E. latifolia* (here including *E. citriodora*), with centers in northern Central America and subtropical South America. Both species have a basic chromosome number of $x = 6$ ($2n = 12$) and a similar bimodal karyotype, which is distinctive in Tigridieae; all other genera of the tribe have $x = 7$. The common form of *E. bulbosa* has a heteromorphic long chromosome pair, the result of a pericentric inversion in one of the long chromosomes, and it is sexually sterile, unlike *E. latifolia*, which is self-compatible and autogamous. The systematics and nomenclature of the two species are dealt with in detail, and the medicinal properties of *E. bulbosa* are outlined.

Eleutherine Herbert (1843), a member of the New World tribe Tigridieae of Iridaceae, comprises low-growing bulbous plants with pleated lanceolate leaves and small, white, evening-blooming flowers. *Eleutherine bulbosa* (Miller) Urban (syn. *E. plicata* (Sw.) Klatt), which extends across South America from Bolivia and southeastern Brazil to the West Indies, has been known since the seventeenth century (Baker, 1892). Currently, Ravenna (1984a) admits two more species, *E. latifolia* (Standley & L. O. Williams) Ravenna of northern Central America and subtropical South America, and *E. citriodora* (Ravenna) Ravenna, from northern Argentina. We recognize only *E. latifolia* and suggest that *E. citriodora* is conspecific with *E. latifolia*. Two more species have been described from Indochina (Gagnepain, 1934), both conspecific with *E. bulbosa*. They are sometimes erroneously thought to be native there and are still occasionally recognized (Schultes, 1990).

The two species of *Eleutherine* are alike in their nearly identical small, white, stellate flowers with free, ascending stamens and relatively long, filiform style arms that extend between the anthers. Vegetatively they share two unusual features, both synapomorphies: a large foliage leaf inserted at the apex of the vegetative part of the stem; and dark red, rather than brown, bulb scales. In other vegetative features, *Eleutherine* accords well with Tigridieae in having a true bulb and plicate foliage leaves, two important synapomorphies for the tribe (Goldblatt, 1990). The common cultivated strain of *E. bulbosa* is sexually sterile for reasons outlined below. It comprises part of the pharmacopeia of several America Indian tribes and may be a clone that has been dispersed by humans from a source in the eastern Andean foothills of Peru, where the most fertile of the few capsulate specimens occur.

In this paper we describe the chromosome cytology of *Eleutherine* and provide evidence that although both species appear to have an unspecialized morphology, the genus is likely to be a derived genus of Tigridieae. A key to the species, complete nomenclature, and descriptions of the species are provided in the systematics section.

MATERIALS AND METHODS

Collections of *Eleutherine* were obtained from wild sources (Table 1) and cultivated at the Missouri Botanical Garden. For cytological study, root tips were pretreated in aqueous m-bromonaphthalene for 4 hours and then fixed in 3 : 1 absolute ethanol–

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ANN. MISSOURI BOT. GARD. 78: 942–949. 1991.

TABLE 1. Chromosome numbers and collection data for species of *Eleutherine* studied. Voucher specimens are located at the Missouri Botanical Garden (MO).

Species	Diploid number	Collection data
E. latifolia	12	Argentina. Tucumán: *Castillo* sub *Goldblatt 9072*
	12	Mexico. San Luis Potosí: Tamazunchale, Howard sub *Goldblatt 9071*
E. bulbosa	12	Peru. Loreto: Pampa Hermosa and vicinity, *Lewis et al. 10624*

glacial acetic acid. After hydrolysis in 10% HCl for 6–7 minutes at ca. 65°C, root tips were squashed in FLP orcein (Jackson, 1972). Karyotypes were drawn with a camera lucida.

Notes on reproductive biology were based on observation of fruit set in greenhouse plants that were not accessible to potential insect pollinators.

OBSERVATIONS

Two populations of *Eleutherine latifolia*, one from Argentina and one from Mexico, are self-fertile, seed-producing plants with a diploid chromosome number of $2n = 12$. They have an identical karyotype (Fig. 1A, C) of one long subtelocentric chromosome pair 5–6 μm long (including secondary constrictions), and five much shorter, submetacentic to acrocentric pairs 1.5–2 μm long. Large satellites are located on the very small short arms of the two long chromosomes. The satellites are ca. 1 μm long and much exceed the short arms of the long chromosomes. Although easily overlooked in contracted metaphase preparations, they are a striking characteristic of the karyotype. In prophase, the satellites are easily mistaken for a pair of small chromosomes. The thin secondary constrictions are difficult to see and are sometimes stretched by manipulation during preparation of squashes such that the satellites lie some distance from the arms to which they are attached.

Plants of *Eleutherine bulbosa* from Peru, apparently sexually sterile, have a karyotype similar to the above *except* that the pair of long chromosomes do not match. The long arms and satellites differ in length (Fig. 1B). The total length of the chromosomes is, as far as we can estimate by linear measurement of camera-lucida-drawn chromosomes, close to, if not the same as the *E. latifolia* populations. Thus, the longer satellite is ca. 2.3 μm long, and the rest of the chromosome including the secondary constriction is ca. 3.5 μm long. The chromosome with the short satellite is ca. 6 μm long, including the satellite, which is ca. 1 μm long, and corresponds in length and morphology to the long chromosomes of *E. latifolia*.

DISCUSSION

CYTOGENETICS

The chromosomes of *Eleutherine latifolia* accord well with those of *E. bulbosa* in the basic features of the karyotype, $x = 6$ with extreme bimodality and a strongly acrocentric long chromosome pair to which are attached large satellites. The karyotype was briefly described by Guerra (1988), based on unpublished observations of A. Kenton, but a detailed description and illustration have not been published until now.

The basic features of the karyotype of *Eleutherine bulbosa* (also reported in the literature as *E. plicata*) are already known (Zaman et al., 1985; Cherian & Kuriachan, 1988—based on plants cultivated in India; Martinez & De Azkue, 1987; Guerra, 1988—based on plants of South American

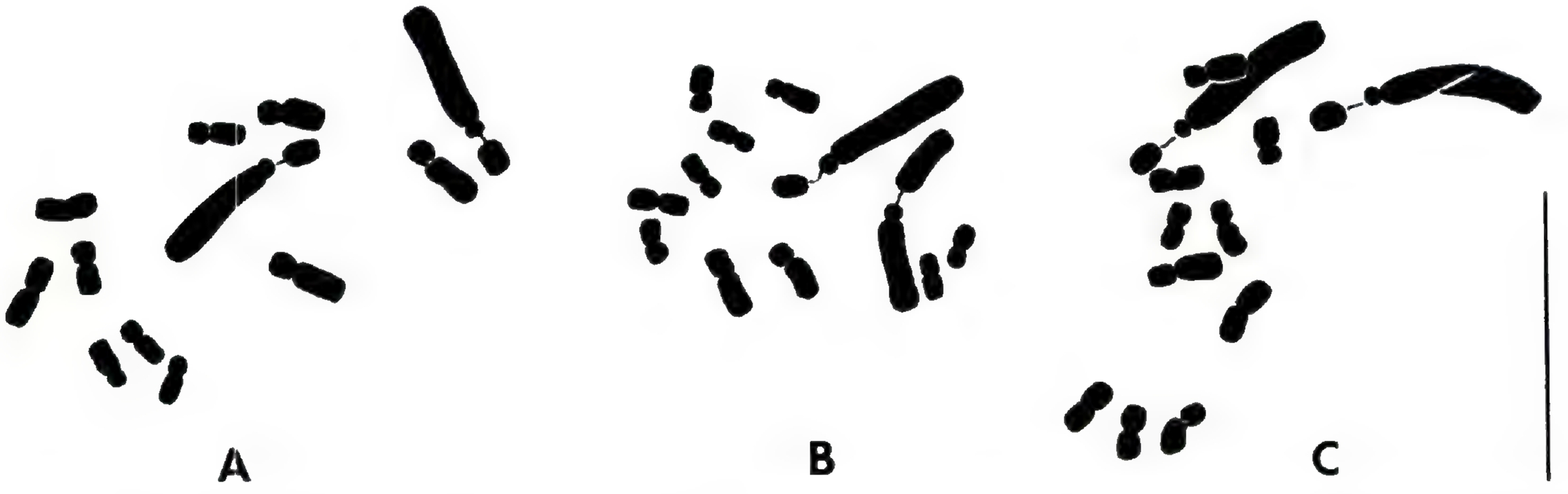


FIGURE 1. Karyotypes of *Eleutherine latifolia* from Mexico (A) and Argentina (C), and *E. bulbosa* (B). (Scale bar = 5 μm.)

origin). *Eleutherine guatemalensis* Standley, which has $2n = 28$ (Ravenna, 1965), is now *Cobana guatemalensis* (Standley) Ravenna. The genus *Cobana* is probably not closely related to *Eleutherine* and belongs in Tigridiinae rather than Cipurinae, where *Eleutherine* seems well placed (Goldblatt, 1982).

The earliest chromosome counts in the literature for *Eleutherine bulbosa* are those of Sharma & Talukdar (1959) and Rao (1969), both papers reporting $2n = 14$ and a karyotype of two long pairs of chromosomes, one of which is metacentric. In the same paper, Sharma & Talukdar (1959) reported $2n = 12$ (and 14) in *Cipura paludosa* Aublet; their drawings of the chromosomes of the two species make it clear that their plants were misidentified. The karyotypes of their so-called *Eleutherine* closely match published karyotypes for *Cipura paludosa* (e.g., Goldblatt, 1982), whereas the karyotypes of their cytotypes of *C. paludosa* correspond with *Eleutherine* here, with some minor variation. The plants studied by Rao (1969) as *Eleutherine* were presumably also misidentified, and their count of $2n = 14$ must be ignored. (*Cipura*, especially *C. paludosa*, is understandably confused with *Eleutherine*, but the two genera are probably not immediately related.)

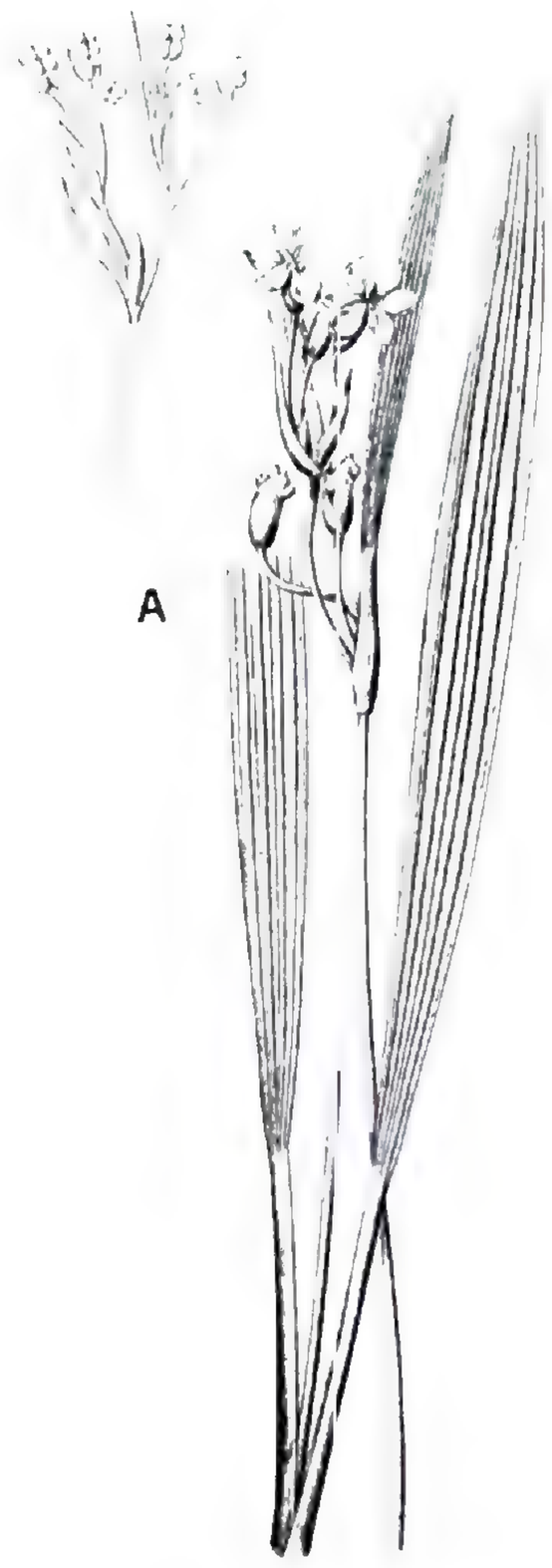
Subsequently, Goldblatt (1982) reported $2n = 12$ and a structurally heterozygous karyotype in *Eleutherine bulbosa*. Zaman et al. (1985) also found $2n = 12$ in *E. bulbosa*, and they reported regular bivalent formation at meiosis and the presence of an inversion bridge with a fragment at meiosis I. Based on this, they postulated that a pericentric inversion in one of the two long chromosomes was responsible for the long chromosome heteromorphism. A fragment associated with a meiotic bridge is not compatible with a pericentric inversion (cf. Stebbins, 1971), but Zaman et al.'s interpretation of the meiotic figures, not illustrated, may not have been correct. A study by Guerra (1988) finally demonstrated convincingly the presence of a pericentric inversion in one of the long chromosomes of *E. bulbosa*, and he also reported a small tandem duplication of part of the short arm of the chromosome with the inversion (and longer satellite), rendering this chromosome slightly longer than its homologue. Guerra's conclusions make the comments of Cherian & Kuriachan (1988) on the nature of the chromosomal restructuring in *E. bulbosa* redundant and need not be repeated here. Despite their refutation of the presence of a pericentric inversion in the species, the meiotic configurations illustrated in their paper show the bridges formed by the long chromosomes without fragments, consistent with heterozygosity for a pericentric inversion.

It is virtually certain that the ancestral karyotype in *Eleutherine* had $x = 6$ and was structurally homozygous, as described here in *E. latifolia* and likely to occur in sexually reproducing *E. bulbosa*, not yet examined cytologically. The mismatched long chromosome pair in the cultivated strain of *E. bulbosa* has a pericentric inversion, which is responsible for its sexual sterility; this accounts for the absence of capsules on most herbarium material of *E. bulbosa* and in cultivated plants. Fertile populations and at least partially fertile individuals do, however, exist. A collection from Peru (*Schunke 971*, NY, F) comprises several individuals, all bearing numerous capsules. Other collections comprise at least one plant with a few developed capsules (*Duss 3836* from Guadelupe, US; *Costa 164* from Pará, Brazil, F; *Faris 475* from Santo Domingo, US). The capsules are small and globose and differ from those of *E. latifolia*, which are oblong to cylindric and always substantially larger.

The basic chromosome number for the entire Tigridieae is probably $x = 7$ (Goldblatt, 1982, 1990; Kenton & Rudall, 1987), and there are few exceptions in the tribe. Only *Gelasine elongata* (Graham) Ravenna (syn. *G. azurea* Herbert fide Ravenna, 1984b) also has $n = 6$ ($2n = 12$) (Kenton & Rudall, 1987). The chromosome number is known in only one other *Gelasine*, *G. uruguayensis*, which has $n = 7$ (Ravenna, 1984c). The karyotype of *G. elongata* has a long acrocentric chromosome pair with conspicuous satellites larger than the short arms (misinterpreted by Goldblatt, 1982, as a pair of small chromosomes), and in this respect resembles *Eleutherine*. However, *G. elongata* differs in having a second relatively long chromosome pair. The karyotype of *G. elongata* is structurally heterozygous, and the chromosomes form a ring of 12 at meiosis (Kenton & Rudall, 1987). Karyotypic and cytogenetic differences between *Eleutherine* and *Gelasine elongata* make it seem unlikely that the two share an immediate common ancestor. The $n = 6$ in *G. elongata* most likely originated from ancestors within the genus with $x = 7$. The only other member of Tigridieae that is known to diverge from the basic $x = 7$ is *Cypella plumbea* Lindley, $n = 5$, but other species of the genus have $n = 7$, which is the basic number for *Cypella* (Goldblatt, 1982; Kenton & Heywood, 1984).

SYSTEMATICS AND PHYLOGENY

The two species that we propose to recognize in *Eleutherine* have virtually identical flowers, but



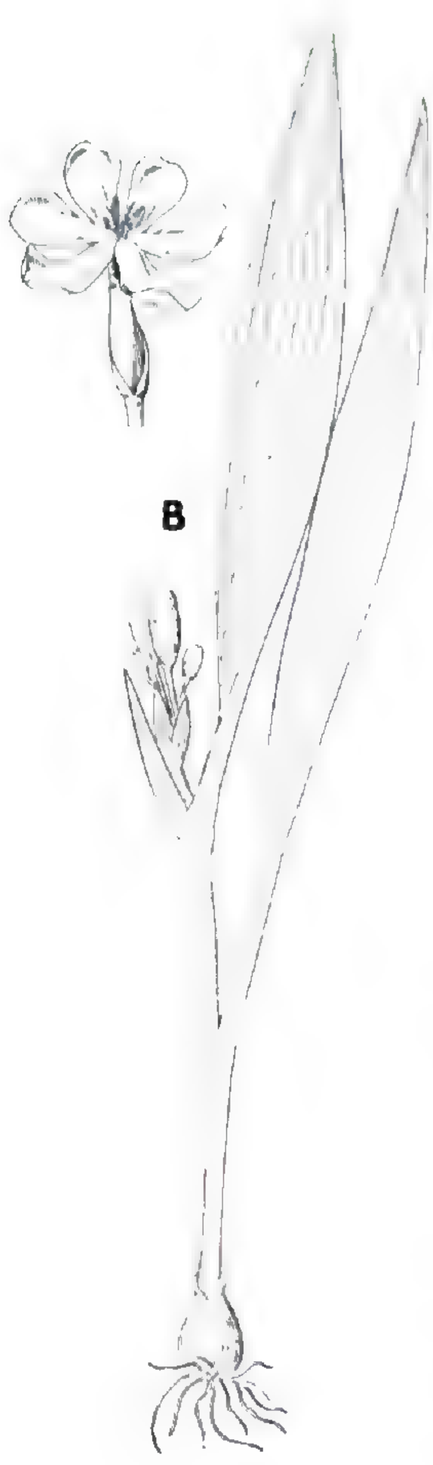


FIGURE 2. Morphology of *Eleutherine bulbosa* (A) and *E. latifolia* (B). Habits × 0.5, flower and fruiting branch of *E. bulbosa* full size.

they are readily distinguished by differences in their inflorescence structure (Fig. 2). In *E. latifolia*, generally a short plant, the large apical cauline leaf subtends one or sometimes two subsessile to shortly pedunculate rhipidia (spathe-enclosed flower clusters), the basic inflorescence type in Iridaceae (Fig. 2B). In *E. bulbosa* the cauline leaf subtends a few pedunculate rhipidia and a secondary axis that terminates in (3–)6–12 rhipidia in umbellate arrangement; thus the rhipidia are arranged in two series, axillary and terminal (Fig. 2A).

The flowers of *Eleutherine* (Fig. 3A) appear to be relatively simple in structure and comparable with those of more primitive genera of Iridaceae. It is tempting to interpret the genus as primitive within Tigridieae, in which a more complex flower structure is the rule. However, Mariceae, sister tribe of Tigridieae, are also characterized by a complex flower structure (Fig. 3B) almost identical with that of Tigridieae (Goldblatt, 1990; Goldblatt & Henrich, 1991), in which the tepals are clawed, the inner tepals have a zone of nectariferous tissue in a fold of the tepal limb, and the thickened style branches are terminally bifurcate and have a sub-

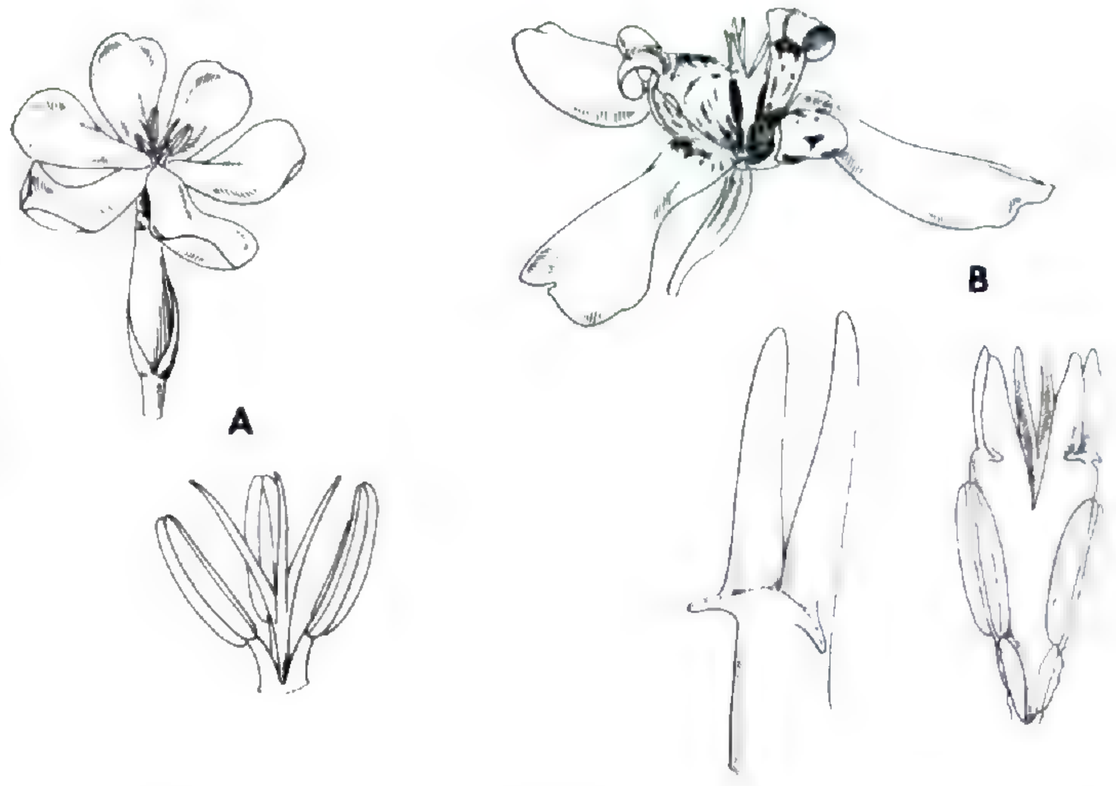


FIGURE 3. Details of the flowers and stamens and style of *Eleutherine* (A) and of the putative ancestral type represented by *Trimezia steyermarkii* (B). Whole flowers full size; details of the separated stamens and styles and style branches much enlarged.

apical transverse stigma. It seems more parsimonious to interpret the flower of *Eleutherine* as derived by a process of reduction in complexity associated with self-compatibility and autogamy, a derived type of reproductive biology in Tigridieae that is basically self-incompatible (Goldblatt, pers. obs.). Similar examples of the simplification of an ancestrally complex flower structure are known within Iridaceae in tribe Irideae, notably in subtribe Homeriinae (Goldblatt, 1979, 1981, 1986). Here, flowers with clawed tepals and elaborate petaloid, apically bifurcate style arms with transverse stigmas, are believed to have been secondarily reduced in several lineages, leading in one genus, *Roggeveldia* Goldblatt, to species with stellate flowers with simple filiform style branches that alternate with the stamens.

SYSTEMATICS

Eleutherine Herbert, Edwards's Bot. Reg. 29: t. 57 (1843). TYPE: *E. plicata* Herbert (= *E. bulbosa* (Miller) Urban).

Galatea Salisb., Trans. Hort. Soc. 1: 310 (1812), nom. nud.

Small, seasonal perennials with a fleshy bulb with reddish tunics. Leaves few, plicate, both basal and cauline, narrowly lanceolate. Stem terete, comprising one long internode, with a large cauline leaf at the apex, subtending the inflorescence. Inflorescences rhipidia, these solitary or several and then arranged in a pseudopanicle; rhipidia (spathe-enclosed umbels) several-flowered, stalked or ± sessile; spathes green, subequal, relatively short. Flower pedicellate, subtended by membranous

bracts as long as the spathes; perianth white, stellate; tepals free, subequal, spreading from the base, without nectaries; filaments free; anthers diverging. Ovary obovoid; style short and dividing opposite the upper half of the filaments, the branches undivided, filiform, extending between the anthers, stigmatic apically. Capsules globose to oblong-cylindric, truncate; seeds angular. Basic chromosome number $x = 6$.

Eleutherine consists of two species distributed in Mexico, West Indies, Central and South America; cultivated in Africa and Asia, especially the Philippines and Indochina, and now naturalized there.

KEY TO THE SPECIES

1a. Plants with several rhipidia per flowering stem, the peduncles borne both in the axils of the cauline leaf and in umbellate fashion on a secondary axis; rarely setting fruit, but capsules globose, 4–6.8 mm long ..... 1. *E. bulbosa*

1b. Plants with 1 or rarely 2 rhipidia either ± sessile or borne on short peduncles inserted in the axil of the cauline leaf; always setting fruit and capsules 12–20 mm long ..... 2. *E. latifolia*

1. Eleutherine bulbosa (Miller) Urban, Repert. Spec. Nov. Regni Veg. 15: 305 (1915). Basionym: *Sisyrinchium bulbosum* Miller, Gard. Dict. ed. 8 (1768). *Galatea bulbosa* (Miller) Britton, Brooklyn Bot. Gard. Mem. 1: 37 (1918) nom. inval., gen. inval. TYPE: uncertain, possibly figure in Burman, Pl. Amer. Fasc. 35 & t. 46 f. 2 (1757 as 1755), but not specifically cited by Miller [perhaps a neotype should be chosen]. [Miller may have had living plants but cited Tournefort, Inst. Rei Herb. 387 (1700), who in turn cited Magnol, Hort. Reg. Monsp. (1697), neither of which has any illustration of the species nor refers to one]. Figure 2A.

Ixia americana Aublet, Hist. Pl. Guiana 1: 33 (1775). *Galatea americana* (Aublet) Kuntze, Revis. Gen. Pl. 2: 701 (1891) nom. inval, gen. inval. *Sisyrinchium latifolium* Sw., Prodr. 17 (1788) nom. illeg. superfl. *Moraea plicata* Sw., Fl. Ind. Occid. 1: 82 (1797) nom. illeg. superfl. *Marica plicata* (Sw.) Ker-Gawler, Curtis's Bot. Mag. 18: t. 665 (1803). *Galatea vespertina* Salisb., Trans. Hort. Soc. 1: 310 (1812) nom. inval., gen. inval. *Cipura plicata* (Sw.) Griseb., Fl. Brit. W. Indian Is. 589 (1864). *Eleutherine* (as *Eleutherina*) *plicata* (Sw.) Klatt in Martius, Fl. Bras. 3(1): 514 & t. 64, f. 2 (1871). TYPE: illustration in Burman, Pl. Amer. Fasc. 35 & t. 46 f. 2 (1757 as 1755).

Eleutherine anomala Herbert, Edward's Bot. Reg. 29: t. 57 (1843). *Galatea anomala* (Herbert) Kuntze, Revis. Gen. Pl. 2: 701 (1891) nom. inval., gen. inval. TYPE: illustration in Bot. Reg. 29: t. 57.

Eleutherine subaphylla Gagnepain, Bull. Soc. Bot. France 81: 66 & f. 67. 1934 et in Fl. Gen. de l'Indo-Chine 6: 676. 1934. TYPE: Vietnam (Annam, Quang-Tri), *Poilane 12279* (P) (a form flowering without basal leaves).

Eleutherine longifolia Gagnepain, Bull. Soc. Bot. France 81: 66. 1934 et in Fl. Gen. de l'Indo-Chine 6: 677. 1934. TYPE: Vietnam (Annam, ? Hué), *Jacquet 611* (P) (described from vegetative plants).

Sisyrinchium americanum, radice phaenicea, foliis plicatis & nervosis etc., Magnol, Hort. Reg. Monsp. 185 (1697).

Bermudiana palmaefolio, radice bulbosa Tournefort, Inst. Rei Herb. 1: 388 (1700).

Sisyrinchium palmifolium sensu Lam., Encyc. Méth. 1: 408 (1783-85) et sensu Cavanilles, Diss. 6: 348 & t. 191 (1788) non Linneaus, Mantissa Pl. 122 (1767) (= *S. palmifolium* L.). (Also *Moraea palmifolia* sensu Jacquin, Icon. Pl. Rar. 2: t. 227 (1790), non sensu Linnaeus; *Eleutherine palmifolia* sensu Merrill, Philipp. J. Sci. 7: 233 (1912) non sensu Linnaeus).

Plants 15–75 cm high, usually sexually sterile and lacking capsules; other characters as for the genus except the following. Inflorescence of several stalked rhipidia, the peduncles borne both in the axil of the cauline leaf and in umbellate fashion on a secondary axis; spathes 11.5–15(–20) mm long; peduncles (12–)20–55 cm long. Tepals 10–18 mm long. Filaments 2–2.5 mm long; anthers 3.5–4.5 mm long. Capsules irregularly globose, showing the outline of the seeds, (2.5–)4–6.8 mm long, seeds rarely more than 3 per locule; seeds 1.8–2.7 mm long, irregularly globose with a concave chalazal end, reddish brown to black (? with age), strongly rugose. Chromosome number $2n = 12$.

Eleutherine bulbosa is widespread, extending from southeastern Brazil and Bolivia to Venezuela and the West Indies (Fig. 4). The original habitat is uncertain. The most consistently fertile plants we have seen are from a population in the eastern Andean foothills of Peru, but occasional plants with capsules are known from eastern Brazil (Pará), Trinidad, Guadeloupe, and Santo Domingo. The branched inflorescence and, when present, the small, more or less globose capsules distinguish the species from its close relative *E. latifolia*. In its extended and branched inflorescence, we assume *E. bulbosa* is the less specialized species. The flowers of the two are essentially identical.

The several specimens sampled cytologically (see discussion of cytology), all sexually sterile, have the two long chromosomes heteromorphic and heterozygous for a pericentric inversion and a tandem duplication, which accounts for the prevalent re-

FIGURE 4. Distribution of *Eleutherine latifolia* (triangles) and *E. bulbosa* (circles).

productive sterility. Chromosomes have not been examined in any fertile plants.

Nomenclatural history. The systematics of this relatively uniform species is remarkably complex. Although first described by Phillip Miller in 1768 in the genus *Sisyrinchium*, his epithet was overlooked by Aublet (in 1775), who named the plant *Ixia americana*, and by Swartz, who gave it two epithets, *Sisyrinchium latifolium* in 1788 and *Moraea plicata* in 1797. All three species were based on the same type. Herbert's (1843) *Eleutherine anomala* was based on plants grown in Britain. Herbert was aware of the four earlier epithets for the species and regarded *E. anomala* as distinct from them. Herbert provided a generic name for plants that had until 1843 been assigned to no less than five genera, if Salisbury's nomen nudum for the genus, *Galatea*, is included. Curiously, Herbert designated *Marica plicata* as the type of *Eleutherine* but did not make the combination *E. plicata* often attributed to him. Adding to the complexity is Lamarck's use of Linnaeus's *Sisyrinchium palmifolium* for *E. bulbosa*. *Sisyrinchium palmifolium* must be based on a specimen collected by Ardouin in Brazil (a species of *Sisyrinchium* still known by this name) rather than on the figure of *E. bulbosa* in Burman's *Plantae Americanae* that Linnaeus cited with a query, in the protologue of *S. palmifolium*. Lamarck's use of the epithet *palmifolium* for *E. bulbosa* was followed by Jacquin (1790), who referred the species to the African *Moraea*, and Merrill (1912), among others.

In 1934, Gagnepain described two more *Eleutherine* species from Indochina that are obviously forms of *Eleutherine bulbosa*: *E. subaphylla*, which

lacks foliage leaves; and *E. longifolia*, which lacks flowers. Specimens matching both are routinely encountered in herbarium material from the Americas, sometimes from populations that include plants of more normal appearance.

Eleutherine bulbosa is an important element of American Indian pharmacopeia and is one of few neotropical Iridaceae with known medicinal uses (Schultes, 1990). It is often cultivated in gardens maintained by Indian tribes (W. Lewis, pers. comm.) and is also fairly widely grown in the tropics as an ornamental. It is used as a vermifuge in Ecuador (Vickers & Plowman, 1984) and is widely documented in the literature and in herbaria as a treatment for bloody diarrhea (Ayala, 1984), haemorrhagia and open wounds (*Lewis et al. 9966, 10624; Costa 164; Peters & Padoch 137; Hahn & Tredwell 125*), and even as a contraceptive (*Schunke 971*). *Eleutherine bulbosa* is now naturalized in the Philippines and Indochina and cultivated in Kwazulu, South Africa (A. Hutchings, pers. comm.), where it is also used medicinally. Quisumbing (1951) recorded the use of *E. palmifolia* (i.e., *E. bulbosa*) as a diuretic in the Philippines. It is also believed to have magical and hallucinatory properties. Schultes (1990) has provided information about chemistry and possible active principles, so far hardly investigated.

2. Eleutherine latifolia (Standley & Williams) Ravenna, Phytologia 56: 195 (1984). *Cipura latifolia* Standley & Williams, Ceiba 1: 75 (1950). TYPE: Honduras, El Zamorano, grounds of the Escuela Agrícola Panamericana, 14 Aug. 1947, *Molina 498* (holotype, EAP). Figure 2B.

Eleutherine citriodora (Ravenna) Ravenna, Phytologia 56: 195 (1984), syn. nov. *Eleutherine bulbosa* subsp. *citriodora* Ravenna, Bol. Soc. Argent. Bot. 10 : 314 (1965). TYPE: Argentina, in pratis urbi Tucumán, Feb. 1964, *Vervoorst s.n.* (holotype, Herb. Ravenna 285 n.v.).

Plants (6–)12–20 cm high, other characters as for the genus except the following. Inflorescence of one, rarely two, subsessile or stalked rhipidia borne in the axil of the cauline leaf; peduncle 10–50(–80) cm long; spathes 15–20 mm long. Tepals 12–14 mm long, 6–8 mm wide. Filaments 2.5–3 mm long; anthers 3 mm long. Style ca. 2 mm long, the branches ca. 4 mm long. Capsules obovoid to oblong-cylindric, 10–28 mm long, with numerous seeds per locule; seeds 2.1–2.3 mm long, conical, the sides somewhat flattened, lightly rugose, dull greenish yellow, dark brown at the chalazal end. Chromosome number $2n = 12$.

Eleutherine latifolia is widespread but scattered in the Neotropics and subtropics, with centers in northern Central America and Mexico and in southern South America, northern Argentina, Paraguay (Fig. 4), and according to Ravenna (1984a), Bolivia, but also recorded in Venezuela. The species is strongly autogamous. Because of the inflorescence that comprises one or occasionally two rhipidia, compared with the several in pseudopaniculate arrangement in *E. bulbosa*, we consider *E. latifolia* to be more specialized.

Until now, *Eleutherine latifolia* has been regarded as a Central American–Mexican endemic. However, the differences between this and the southern South American *E. citriodora* seem to us too trivial to merit continued separation. Herbarium specimens cannot as a rule be distinguished, although Central American plants are often sturdier. In cultivated samples of single populations from Mexico and from Argentina we noted that the Mexican plants have firmly erect stems, clear green foliage, and flowers lightly acrid-smelling, slightly smaller, and opening earlier in the evenings than the plants from Argentina. The latter have stems that seldom remain erect as the capsules develop, the leaves have a slightly bluish tinge and the flowers, faintly sweet-scented, open a full hour later that the Mexican plants, 6:00–6:30 P.M., and last about an hour later, till nightfall, 8:00–8:30 P.M. We have no information on interpopulational variation (flowers are rarely preserved in dry specimens and floral odor is never recorded) in either of the two main centers of the species nor in plants from Venezuela. Thus, at least on available information, we recommend including *E. citriodora* in *E. latifolia*. The only realistic way to tell the two apart is to know their geographic origin. The differences enumerated above are cryptic and can only be seen in live plants: even then we do not know how consistent they are across populations. Experience in other Iridaceae is that flower size, odor, and phenology will often vary to some extent in widely distributed species.

When Ravenna described *Eleutherine citriodora* as *E. bulbosa* subsp. *citriodora*, he distinguished it from subspecies *bulbosa* by its somewhat larger rhipidial spathes crowded in the axil of the cauline leaf; the oblanceolate, more acute, tepals; the flowers citrus-scented; and the stamens often suberect. This distinction is the same as that between the Central American *E. latifolia* and *E. bulbosa*, except for the sweet floral scent in so-called *E. citriodora* from Argentina. We have not seen the type of *E. citriodora*, which is in the private collection of P. Ravenna and is unavailable

for study. Our interpretation of the taxon is therefore based on the diagnosis and the locality information. The type collection was made near the town of Tucumán, northern Argentina, where plants corresponding to *E. latifolia* are well known, whereas *E. bulbosa* does not occur in Argentina. Unlike the closely related *E. bulbosa*, there are no recorded human uses of *E. latifolia*.

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SULCUS AND OPERCULUM STRUCTURE IN THE POLLEN GRAINS OF IRIDACEAE SUBFAMILY IXIOIDEAE[1]

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ABSTRACT

Ixioideae, the largest and most derived of the four subfamilies of Iridaceae, is distinct in the family in having specialized pollen grains with tectate-perforate and scabrate sculpturing. This is in contrast to the prevailing tectate-reticulate exine in the rest of the family and its putative allies. In addition, most species have monosulcate grains with a 2-banded operculum, a feature that is probably synapomorphic for the subfamily. Exceptions among taxa with monosulcate grains having either a 1-banded or disorganized operculum are seen as most probably derived. Important exceptions to this pattern are *Micranthus*, which has zonasulcate grains with reticulate exine; one of seven species of *Thereianthus*, *T. racemosus*, which also has a reticulate exine except on the operculum; *Zygotritonia*, which has 3-aperturate inoperculate grains; and *Savannosiphon*, in which the grains have an irregular distribution of the exine and may be described as inaperturate but functionally omniaperturate. The origin of the operculum and the significance of the variation within Ixioideae is considered in relation to the systematics of Ixioideae.

Ixioideae, the largest of the four subfamilies of Iridaceae, are generally considered to have relatively uniform pollen grain morphology (Schulze, 1970, 1971; Goldblatt, 1990), and pollen has been accorded scant attention in systematic investigations of the 28 genera and ca. 860 species that are now considered to comprise the subfamily (Goldblatt, 1991). Like most petaloid monocots, pollen grains of Iridaceae are usually sulcate, and the exine is tectate-columellate. A reticulate surface pattern is probably basic for Iridaceae (Goldblatt, 1990; J. Walker, pers. comm.) and is the predominant or exclusive condition in Isophysidoideae, Nivenioideae, and Iridoideae, three of the four subfamilies recognized by Goldblatt (1990). However, in Ixioideae, most species of most genera have a perforate (micropunctate) and scabrate (spinulate) exine, a synapomorphy for the subfamily (Goldblatt, 1990, 1991). Within Ixioideae, *Syringodea* and *Crocus* have an imperforate scabrate exine, while in the relatively specialized *Micranthus* the exine is reticulate (Erdtman, 1952; Schulze, 1971). In *Syringodea* the grains are inaperturate and in *Crocus* inaperturate, spiraperturate, or polyrugoidate, clearly derived states for these two very specialized genera. The grains of *Micranthus* have been described as syncolpate by Schulze (1970).

A preliminary study of the pollen grains of *Micranthus* and the putatively closely related *Thereianthus* (Goldblatt, 1989a) to compare in detail the exine patterning revealed two unusual features. In *Thereianthus* there are discrete bands of exine in the sulcus, clearly separate from the rest of the exine. This structure, which accords with a broad definition of an operculum, is not present in *Micranthus*. The grains of the latter are zonasulcate (perhaps equivalent to Schulze's term syncolpate) in all three species. Independent study of the biology of North African species of *Romulea* (Bari, in prep.) revealed the presence of opercula in these species as well. These observations prompted us to examine the pollen grain aperture in a selection of species of all genera of Ixioideae. The size of Ixioideae precludes an examination of every species, but our results suggest that although the aperture is variable in the subfamily, its structure is constant within most genera so that a more thorough survey seems unnecessary except perhaps in the course

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of detailed systematic research. We have included observations of exine patterning and grain size as well as sulcus structure in our results.

Materials and Methods

For examination of the sulcus, 80 species in 26 of the 28 genera (Tables 1, 2) of Ixioideae were examined (*Crocus* and *Syringodea*, with imperforate grains, were not included in the survey). Information extracted from the literature for another five species (Radelescu, 1970a, b) is also included in Table 1.

Pollen grains from either fresh or herbarium material were placed on glass slides, rinsed briefly with 70% ethanol, and then mounted in Calberla's fluid (Ogden et al., 1974), which effectively re-expanded collapsed grains and stained the exine dark pink while leaving the rest of the grain unstained. Pollen was taken from herbarium specimens collected no more than 20 years ago whenever possible, as grains from older specimens were found to re-expand poorly, if at all. Grains were examined under the light microscope and measured within 48 hours of preparation for the following characters: aperture condition and presence and form of the operculum (Table 1); polar and equatorial diameter, sulcus width and length, operculum (if present) width and length, and interopercular distance when the operculum was 2-banded (Table 2). Measurements (Table 2) represent the mean of 5–10 grains. Descriptive terminology used follows Walker & Doyle (1975).

For grains examined under the scanning electron microscope (SEM), the following method was followed. Fresh grains were fixed in FAA, and dried grains from herbarium specimens were rehydrated by warming in 10% KOH for ca. 10 minutes. The grains from either source were then dehydrated directly in ethanol and critical-point dried before mounting and coating. Specimens were observed at an accelerating voltage of 15–20 kV.

Observations

Aperture

All genera examined (Table 1) except *Micranthus*, *Savannosiphon*, and *Zygotritonia* have monosulcate pollen grains (Figs. 1A, B, 2–5). The sulcus is relatively broad and when expanded is usually as wide as the grain or nearly so (Table 2). *Syringodea* (10 spp.) and *Crocus* (80 spp.), which have specialized, inaperturate and inaperturate, spiraperturate, and polyrugoidate grains, respectively (Erdtman, 1952; Schulze, 1971; de Vos, 1974a; Mathew, 1982), were not included in our study.

Zygotritonia has grains with three elliptic apertures and thus is evidently trisulcate (Fig. 1C). The apertures are equidistant from one another and run almost the entire length of the ellipsoid grains.

The more or less spherical grains of the monotypic tropical African *Savannosiphon* have an irregular distribution of exine (Fig. 1D). The overall impression is of random distribution of irregularly shaped stained (exinous) patches of varying size and unstained (nonexinous) wall material. The grains are evidently inaperturate in morphological terms but probably functionally omniaperturate. Since grains of plants from two separate populations were examined, the possibility that our sampling was not representative seems unlikely.

In *Micranthus* the grains of all three species are evidently zonasulcate (Figs. 6, 8). The aperture is ca. 18–20 μm wide and forms a continuous band around the grain. We could not determine the orientation of the aperture but assume that it is polar rather than equatorial. There is a fair amount of scattered, granular exine material within the sulcus, usually concentrated close to the sulcus margins (Fig. 8).

Operculum

In most of the genera with sulcate grains (Table 1) there are two narrow, linear to narrowly elliptic bands of exine within the sulcus (Figs. 1A, 2). By definition, this discrete exinous structure within the sulcus constitutes an operculum (cf. Kremp, 1965; Faegri & Iversen, 1964). The opercular exine appears to have the same microstructure as the rest of the grain (Figs. 2–5). These more or less parallel bands, occasionally joined at their ends, constitute an unusual structure that apparently does not occur in Iridaceae outside Ixioideae. Included among the species listed in Table 1, we note from figures provided by Radelescu (1970a, b) that the following also have a 2-banded operculum: *Crocosmia* × *crocosmiiflora* (Lemaire ex Morren) N.E. Br., *Gladiolus illyricus* Koch, *G. vandermerwei* (L. Bolus) Goldblatt & de Vos, *G. imbricatus* L., *Sparaxis tricolor* (Schneev.) Ker, and *Tritoniopsis pauciflora* (Jacq.) G. Lewis.

Exceptions to the above pattern among Ixioideae with sulcate grains are as follows. All four species of *Ixia* examined and also *I. purpureorosea* G. Lewis (Radelescu, 1970a), *Anomatheca viridis* and *A. fistulosa* (but not the other three species of the genus), five of the seven species of *Thereianthus*,

TABLE 1. Pollen grain sulcus and operculum type for Ixioideae, including data from Radelescu (1970a, b). Collection information for the species examined here is included in the table. Taxa are arranged alphabetically by genus and species, following the most current taxonomy for the subfamily (Goldblatt, 1991). m/s = monosulcate; z/s = zonasulcate; t/c = tricolpate; s/u = structure uncertain (see text); 2/b = two-banded; 1/b = one-banded; d/o = disorganized; a = absent. All vouchers are housed at the Missouri Botanical Garden Herbarium (MO) unless stated otherwise. Total species per genus is indicated in parentheses after the genus name.

Taxon	Aperture	Operculum	Collection data
Anomatheca (5)			
fistulosa (Klatt) Goldblatt	m/s	1/b	*Goldblatt 2359*
grandiflora Baker	m/s	2/b	*Jansen 7879*
laxa (Thunb.) Goldblatt	m/s	2/b	ex hort. no voucher
verrucosa (Vogel) Goldblatt	m/s	2/b	*Goldblatt 2933*
viridis (Aiton) Goldblatt	m/s	1/b	*Goldblatt 3640, 7190*
Babiana (62)			
dregei Baker	m/s	2/b	*Lavranos 22231*
stricta (Aiton) Ker	m/s	2/b	*Goldblatt 2322*
Chasmanthe (3)			
aethiopica (L.) N.E. Br.	m/s	2/b	*Goldblatt 1716*
Crocosmia (8)			
aurea (Pappe ex Hook.) Planchon	m/s	2/b	*Phillips 4670b*
×*crocosmiiflora* (Lem. ex Morren) N.E. Br.	m/s	2/b	Radelescu (1970a)
Devia (1)			
xeromorpha Goldblatt & Manning	m/s	2/b	*Snijman & Manning 1194*
Dierama (44)			
cooperi N.E. Br.	m/s	2/b	*van der Zeyde 63*
mosscii (N.E. Br.) Hilliard	m/s	2/b	*Mauve & Venter 1*
pendulum (L.f.) Baker	m/s	2/b	*Dahlstrand 2896*
Duthieastrum (1)			
linifolium (Baker) de Vos	m/s	2/b	*Acocks 24202* (K)
	m/s	2/b	*Acocks 460* (BOL)
Freesia (11)			
occidentalis L. Bolus	m/s	2/b	*Goldblatt 4069*
refracta (Jacq.) Klatt	m/s	2/b	*Goldblatt 2841*
Geissorhiza (82)			
schinzii (G. Lewis) Goldblatt	m/s	2/b	*Goldblatt 3008*
scillaris A. Dietr.	m/s	2/b	*Walters 2616*
Gladiolus (215)			
abyssinicus (Brongn. ex Lemaire) Goldblatt & de Vos	m/s	2/b	*Lavranos & Collonette 20357*
callianthus Marais	m/s	2/b	*Keeley s.n.*
communis L.	m/s	2/b	Martín Cacao & Fernández (1990)
decoratus Baker	m/s	2/b	*Richards 18743* (P)
dehnianus Merxm.	m/s	2/b	*Chase 8016* (P)
dalenii Geel	m/s	2/b	*Ryding s.n.* (UPS)
erectiflorus Baker	m/s	2/b	*La Croix 1034*
grantii Baker	m/s	2/b	*Polhill & Paulo 1218* (P)
gunnisii (Rendle) Marais	m/s	2/b	*Bally & Melville 15706*
illyricus Koch	m/s	2/b	Radelescu (1970b), Martín Cacao & Fernández (1990)
imbricatus L.	m/s	2/b	Radelescu (1970b)
italicus Miller	m/s	2/b	Martín Cacao & Fernández (1990)

TABLE 1. Continued.

Taxon	Aperture	Operculum	Collection data
melleri Baker	m/s	2/b	*Goldblatt et al. 8135*
muenzneri Harms	m/s	2/b	*Pawek 10432*
vandermerwei (L. Bolus) Goldblatt & de Vos	m/s	2/b	Radelescu (1970b)
Hesperantha (ca. 65)			
humilis Baker	m/s	2/b	*Goldblatt 6090*
radiata (Jacq.) Ker	m/s	2/b	*Goldblatt 6994*
Ixia (45)			
brevituba G. Lewis	m/s	1/b	*Goldblatt & Manning 8645*
polystachya L.	m/s	1/b	*Goldblatt 3254*
purpureorosea G. Lewis	m/s	1/b	Radelescu (1970a)
rapunculoides Delaroche	m/s	1/b	*van Berkel 140*
scillaris L.	m/s	1/b	*Goldblatt 2567*
Lapeirousia (36)			
arenicola Schltr.	m/s	2/b	*Compton s.n.*
coerulea Schinz	m/s	2/b	*Lavranos 22698*
erythrantha Baker	m/s	2/b	*Goldblatt 7515*
neglecta Goldblatt	m/s	2/b	*Goldblatt & Manning 9022*
Melasphaerula (1)			
ramosa (L.) N.E. Br.	m/s	2/b	*Low 943*
Micranthus (3)			
alopecuroides (L.) Ecklon	z/s	a	*Barker 4903* (NBG)
junceus (Baker) N.E. Br.	z/s	a	*Winkler 166* (NBG)
tubulosus (Burm.f.) N.E. Br.	z/s	a	*Goldblatt 8711*
Pillansia (1)			
templemannii L. Bolus	m/s	2/b	*Goldblatt 7907*
Radinosiphon (1-2)			
leptostachya (Baker) N.E. Br.	m/s	2/b	*Goldblatt 5933, 6864*
cf. *leptostachya*	m/s	d/o	*Goldblatt s.n.*
Romulea (90)			
bifrons Pau	m/s	2/b-d/o	*Moret & Bari 12-08*
bulbocodium (L.) Sebast. & Mauri	m/s	2/b (joined)	*Moret & Bari 313-89*
var. *dioica* Batt.	m/s	2/b	*Moret & Bari 413-89*
camerooniana Baker	m/s	2/b	*Gereau & al. 2828*
clusiana (Lange) Nyman	m/s	2/b	Martín Cacao & Fernández (1990)
columniae Sebast. & Mauri	m/s	d/o	*Moret & Bari 29-38*
engleri Bég.	m/s	1/b–2/b (joined)	*Moret & Bari 311-12*
ligustica Parl.	m/s	2/b	*Moret & Bari 52-88*
major Schousboe	m/s	2/b (joined)	*Moret & Bari 743-89*
monadelpha (Sweet) Baker	m/s	2/b	*Goldblatt 4036*
ramiflora Ten.	m/s	2/b	Martín Cacao & Fernández (1990)
rollii Parl.	m/s	d/o	Moret & Bari 443-89
rosea (L.) Ecklon	m/s	2/b	Williams 2514
stenopetala Bég.	m/s	2/b	Moret & Bari 14-18
Savannosiphon (1)			
euryphylla (Harms) Goldblatt & Marais	s/u	s/u	*Draper 14* (K); *Pawek 7972*
Schizostylis (1)			
coccinea Backh. & Harv.	m/s	2/b	*Gibbs Russel 3016*

TABLE 1. Continued.

Taxon	Aperture	Operculum	Collection data
Sparaxis (13)			
bulbifera (L.) Ker	m/s	2/b	*Williams 430*
caryphyllacea Goldblatt	m/s	2/b	*Goldblatt 6162*
galeata Ker	m/s	2/b	*Goldblatt 7234A*
grandiflora (Delaroche) Ker	m/s	2/b	*Goldblatt 6270*
tricolor (Schneev.) Ker	m/s	2/b	Radelescu (1970a)
Thereianthus (7)			
bracteolatus (Lam.) G. Lewis	m/s	1/b	*Grant 4244*; *Goldblatt 9032*
ixioides Lewis	m/s	1/b	*Pillans 10276*
juncifolius (Baker) G. Lewis	m/s	2/b	*Esterhuysen 32359*; *Jackson s.n.*
longicollis (Schltr.) G. Lewis	m/s	1/b	*Compton 12413* (NBG)
minutus (Klatt) G. Lewis	m/s	1/b	*Esterhuysen 35830*; *Goldblatt 5221*
racemosus (Klatt) G. Lewis	m/s	2/b(–1/b)	*Esterhuysen 16620* (BOL)
spicatus (L.) G. Lewis	m/s	1/b	*Goldblatt 5396, 9032*
Tritonia (28)			
dubia Ecklon ex Klatt	m/s	2/b	*Goldblatt 4944*
pallida Ker	m/s	2/b	*Goldblatt 4167*
Tritoniopsis (22)			
pauciflora (Jacq.) G. Lewis	m/s	2/b	Radelescu (1970a)
pulchella G. Lewis	m/s	2/b	*Goldblatt 6839*
Watsonia (52)			
aletroides (Burm.f.) Ker	m/s	2/b	*Goldblatt 2858*
borbonica (Pourret) Goldblatt	m/s	2/b	*Goldblatt 7918*
marginata (L.f.) Ker	m/s	2/b	*Snijman 972*
Zygotritonia (4)			
bongensis (Pax) Mildbr.	t/c	a	*Fay 5544*
nyassana Mildbr.	t/c	a	*Faden & Faden 74/117*

and one North African species of the predominantly southern African *Romulea* have grains with a single, narrowly elliptical band of exine in the center of the sulcus (Fig. 1B). This resembles the operculum of some genera of Tecophilaeaceae (Simpson, 1985). In *A. viridis*, *Thereianthus minutus* (Fig. 4), and *R. engleri* the opercular band of some grains lacks exine in the median center, suggesting the incomplete fusion of two separate bands. In one sample of *Radinosiphon leptostachya* the sulcus has exine fragments evenly scattered over its entire surface, while in three North African species of *Romulea* the operculum is sometimes partly (*R. bifrons*) to completely disorganized (*R. columnae*, *R. rollii*).

In species with a 2-banded operculum, the bands are separated from one another and from the sulcus margins by the pore membrane that remains unstained in our treatment. There may be scattered, small exine fragments concentrated in the midline of the unstained areas of the sulcus (Figs. 2–5). The opercular bands are two-thirds to nearly as long as the sulcus and converge (rarely appearing fused) at their ends; thus, the interopercular space is widest in the center of the sulcus. The opercular bands range from 3.6–12.5 μm wide and are consistent in width within species and sometimes also within genera, but are fairly variable in length even within species.

GRAIN SHAPE AND SIZE

The grains of most species are typically broadly ellipsoid and slightly longer in equatorial than polar diameter, thus prolate (Table 2), but in a number of genera the grains are more or less globose. Grains of *Micranthus* and *Savannosiphon*, in particular, are spherical when fully expanded. Size is variable among species within genera as well as between genera. The smallest grains recorded are those of *Ixia scillaris* (32 × 36 μm) and the largest those of *Savannosiphon* (106 × 106 μm) and *Micran-*

thus tubulosus (90 × 90 μm). Variation in size within genera may be extensive, notably in *Gladiolus* (Table 2), but so far we have found no taxonomic significance to size per se at the generic level, except that *Ixia* (Table 2) seems consistently to have the smallest grains. The genus stands out in the subfamily in this feature.

EXINE SCULPTURING

The exine of most genera of Ixioideae is tectate-columellate and usually has a perforate, sparsely scabrate tectum (described as punctitegillate or micropunctate and granulate, spinulate or verrucate). Our study did not focus on this aspect of the pollen because it has been extensively documented by Schulze (1970, 1971) using light and transmission electron microscopy and reported under the SEM for *Duthieastrum* (= *Duthiella*) (de Vos, 1974b), *Homoglossum* (now *Gladiolus*) (de Vos, 1976), *Tritonia* (de Vos, 1982), and *Pillansia* (Goldblatt & Stein, 1988).

Exceptions are the three species of *Micranthus* (Figs. 6–8) that have a reticulate tectum (Erdtman, 1952; Schulze, 1970, 1971), which *Thereianthus racemosus* has as well. The operculum of the latter, however, has a perforate exine. *Syringodea* and *Crocus* have an imperforate but sparsely scabrate tectum (Schulze, 1971; de Vos, 1974a).

Descriptions of the exine structure of pollen grains of *Thereianthus* and *Micranthus*, not before examined under the SEM, are as follows.

Thereianthus (Figs. 2–4). Exine tectate-columellate, tectum perforate (except *T. racemosus*), the perforations small (ca. 0.25–0.55 × the width of the intervening tectum, *T. juncifolius*, *T. longicollis*), (ca. 0.75–1 × the width of intervening tectum, *T. minutus*, especially on the proximal pole); finely scabrate; terminating abruptly at the sulcus (*T. minutus*) or broken into scabrate patches (especially *T. juncifolius*). In *T. racemosus*, tectum reticulate, lumina 2–3 × width of the walls, becoming microreticulate at the sulcus margins with the walls as wide as the lumina; exine of the operculum perforate (perforations ca. 0.75–1 × the width of the intervening tectum). Thus, except for *T. racemosus*, the exine of *Thereianthus* is typical of Ixioideae.

Micranthus (Figs. 6–9). Exine tectate-columellate, reticulate entirely or becoming microreticulate to perforate (Fig. 9) toward the margins of the sulcus (especially *M. tubulosus*), and forming isolated scabrate islands near the sulcus margins, the muri finely scabrate, lumina 1–3 × the width of the muri (*M. alopecuroides*), 1.3–4 × (*M. junceus*), 0.75–22.2 × (*M. tubulosus*), floor of the lumina containing pilae.

DISCUSSION

PHYLOGENETIC SIGNIFICANCE AND ORIGIN OF THE OPERCULUM

Operculate pollen has been mentioned as occurring in Ixioideae by Schulze (1970, 1971), who did not indicate which taxa had an operculum nor its specific form. However, figures published by Radelescu (1970a, b) show an operculum in the sulcus of a few species, drawn as somewhat diffuse exinous material. Referring to the operculum as "colpus ornamentation," Radelescu did not describe its structure in detail nor did she include more than a few of the genera possessing an operculum in her survey. A 2-banded operculum is reported by Straka & Friedrich (1984) in *Gladiolus bojeri* (as *Geissorhiza bojeri*) and appears in the SEM micrograph of a pollen grain of a *Gladiolus* cultivar in Kress & Stone (1982). Martín Cacao and Fernández (1990) describe a 2-banded operculum in species of *Romulea* and *Gladiolus* that occur in Spain. The absence of any reference to an operculum (cf. Zavada, 1983) from other studies of the pollen morphology of Iridaceae is probably attributable to the examination of either acetolyzed or unexpanded grains.

The occurrence of an operculum in all 23 genera of Ixioideae that have monosulcate pollen grains (the basic aperture type for the subfamily), including members of all three tribes, makes it all but certain that an operculum is a synapomorphy for Ixioideae. The operculum is present in the 2-banded form in *Pillansia* (the only genus of Pillansieae), in three of the five genera of Watsonieae sensu Goldblatt (1989a, 1990), and in 18 of the 19 genera of Ixieae that have monosulcate pollen grains.

Although for morphopalynological reasons (A. Le Thomas, pers. comm.) it may be preferable to see the 2-banded operculum as having arisen from a 1-banded operculum, the pattern in extant Ixioideae suggests that a 2-banded operculum is ancestral in the subfamily, and this is congruent with what is known about relationships within Ixioideae (Goldblatt, 1990, 1991; Rudall & Goldblatt, in press). The 1-banded operculum of *Ixia* and some species of *Romulea*, *Anomatheca* (all Ixieae) and *Thereianthus* (Watsonieae) must therefore be regarded as derived. The occurrence of the 1-banded operculum is scattered in the subfamily and none

TABLE 2. Pollen grain characteristics of selected Ixioideae (voucher information as in Table 1). Measurements for interopercular distance are only for grains with a double-banded operculum; those with a single operculum are scored n/a (nonapplicable) for the character. Measurements were taken only from normal-looking grains and are the mean of 5–10 measurements for each feature. Equatorial diameters are measured across the length of the sulcus. All measurements in microns.

Taxon	Grain diameter		Sulcus		Operculum		Interopercular distance
	Pole	Equator	Width	Length	Width	Length	
Anomatheca							
fistulosa	57	58	43	>58	4.8	43	n/a
grandiflora	66	76	48	>76	8.4	67	7.2
laxa	60	64	48	>64	7.2	63	9.6
verrucosa	53	61	34	>61	4.8	48	8.4
viridis	76	87	58	>87	12.5/6.3	60	n/a/2.4
	51	59	34	>59	12.1	39	n/a
Babiana							
dregei	63	67	43	>67	6.6	51	12.1
stricta	76	89	48	>89	7.2	58	10.8
Chasmanthe							
aethiopica	52	59	34	53	8.4	48	9.6
Crocosmia							
aurea	43	57	48	>57	4.8	48	12.1
Devia							
xeromorpha	46	52	34	>52	3.6	35	8.4
Dierama							
cooperi	46	53	29	>53	4.8	39	6.0
mossii	48	51	41	>51	6.0	41	9.6
pendulum	68	65	60	>65	10.4	58	16.9
Duthieastrum							
linifolium	55	75	51	>75	7.9	70	12.1
Freesia							
refracta	51	58	36	>58	6.5	41	10.8
Geissorhiza							
schinzii	89	96	65	>96	8.5	43	19.3
scillaris	44	48	36	>48	4.8	35	11
Gladiolus							
abyssinicus	60	65	43	>65	8.4	58	8.4
callianthus	75	82	43	>82	8.4	68	12.1
decoratus	59	60	31	>66	5.1	44	8.8
dehnianus	37	40	31	>40	6.6	42	5.9
erectiflorus	60	71	53	>71	9.6	51	9.6
grantii	50	53	47	>53	5.9	47	7.4
muenzneri	43	48	40	>48	7.2	27	7.2
melleri	47	58	34	>58	6.0	48	7.2
Hesperantha							
humilis	51	51	43	>51	4.5	38	12.5
radiata	48	48	27	>48	4.1	36	6.0
Ixia							
brevituba	32	36	24	>36	4.8	27	n/a
polystachya	34	38	23	>38	9.6	36	n/a
rapunculoides	37	41	27	>41	8.4	36	n/a
scillaris	30	41	27	>41	6.6	39	n/a

TABLE 2. Continued.

Taxon	Grain diameter		Sulcus		Operculum		Inter-opercular distance
	Pole	Equator	Width	Length	Width	Length	
Lapeirousia							
arenicola	67	72	48	>72	6.0	60	15.7
coerulea	55	55	36	>55	4.8	36	9.1
erythrantha	51	65	38	>65	3.6	53	7.2
Melasphaerula							
ramosa	55	61	34	>61	4.9	53	7.2
Micranthus							
tubulosus	90	90	18–20	n/a	n/a	n/a	n/a
Pillansia							
templemannii	63	67	65	>67	9.6	60	9.6
Radinosiphon							
leptostachya	64	71	36	>71	6.2	71	8.2
Romulea							
camerooniana	55	60	48	>60	6.0	41	8.4
monadelpha	43	62	24	>62	5.3	43	9.6
rosea	46	63	25	>63	4.8	43	7.2
Savannosiphon							
euryphylla	106	106	n/a	n/a	n/a	n/a	n/a
Schizostylis							
coccinea	48	55	30	>55	7.2	43	4.8
Sparaxis							
bulbifera	70	77	48	>78	8.9	60	12.7
grandiflora	58	67	46	67	6	65	15.7
Thereianthus							
juncifolius	65	70	41	65	6.0	57	7.2
	79	76	43	>76	6.6	58	9.6
minutus	55	70	53	>70	19.9	58	n/a
racemosus	43	58	51	>58	4.8	43	8.4
spicatus	68	71	55	>71	12.1	65	n/a
Tritonia							
pallida	59	70	36	>70	6.0	53	8.4
Tritoniopsis							
pulchella	54	59	53	±59	9.6	53	15.6
Watsonia							
aletroides	63	71	58	>71	12.5	60	16.9
borbonica	87	101	58	>101	8.9	60	10.4
marginata	63	69	68	>69	8.4	55	18.1
Zygotritonia							
bongensis	63	70	17	>70	n/a	n/a	n/a
nyassana	48	57	12	>57	n/a	n/a	n/a

of the genera in which it occurs is especially primitive. *Romulea* is probably a particularly specialized genus. Moreover, the closest relatives of genera with a 1-banded operculum have a 2-banded operculum.

STATUS OF TAXA WITH 1-BANDED OPERCULA

The single opercular band in *Anomatheca fistulosa* and the single or nearly single band in *A. viridis* are noteworthy, for these two species are

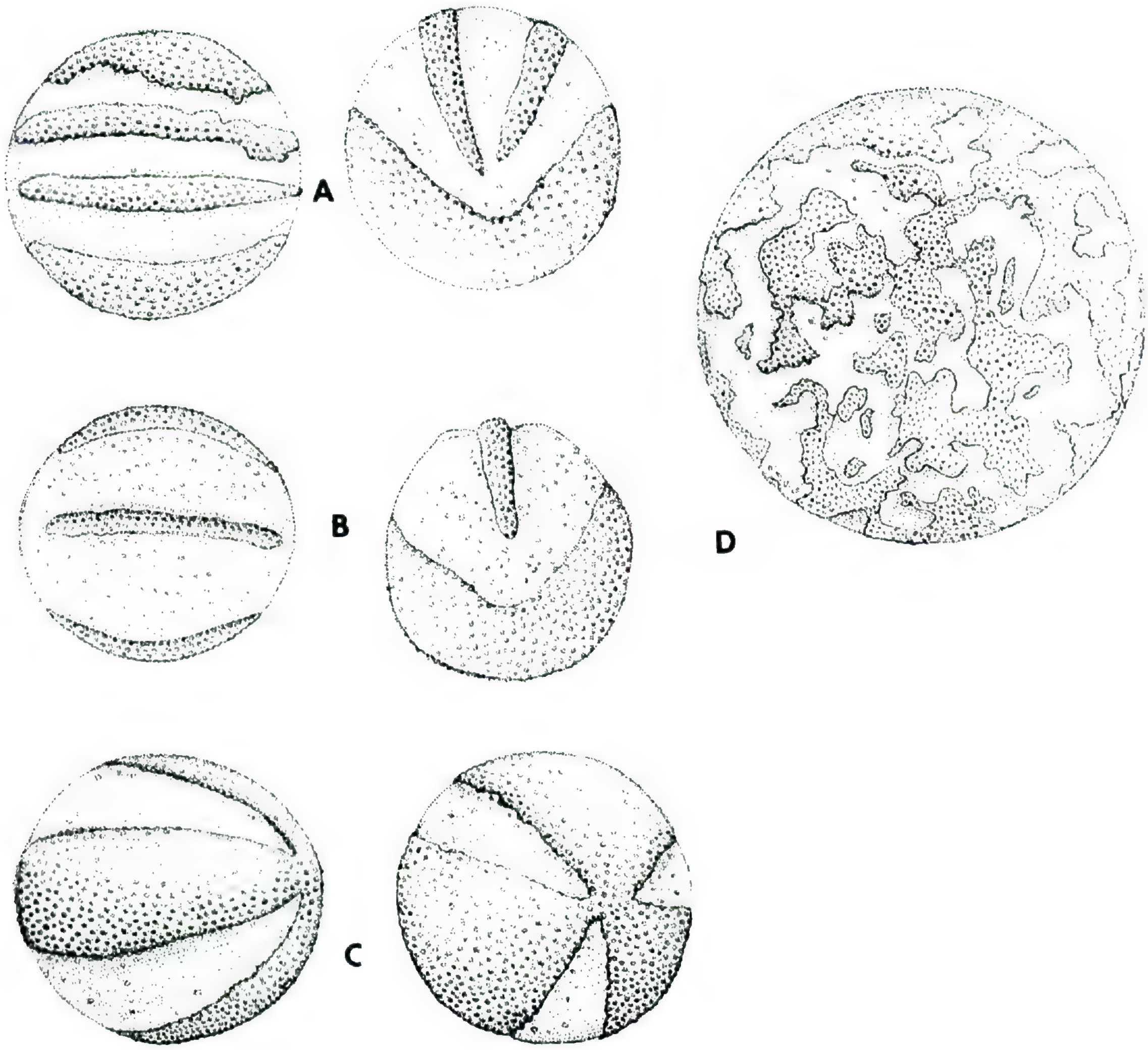
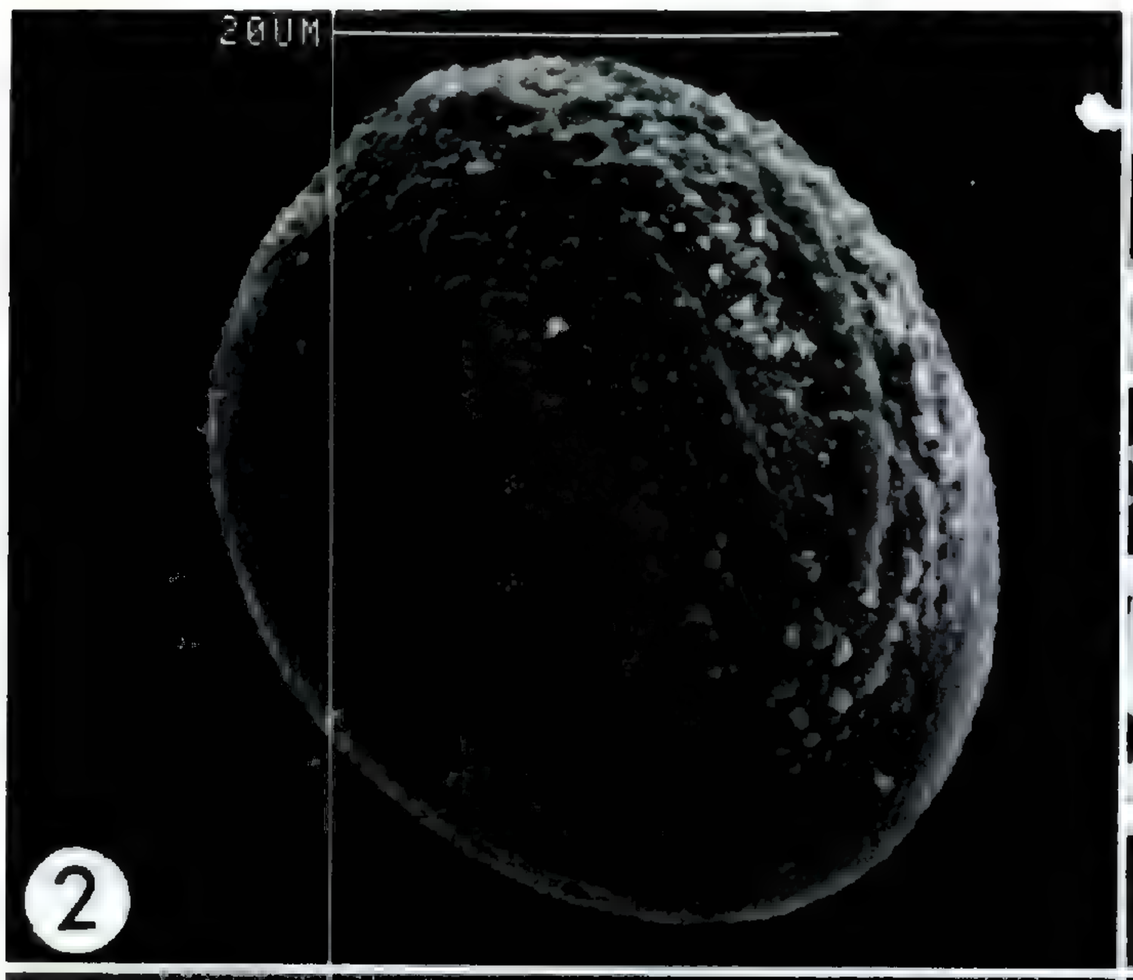


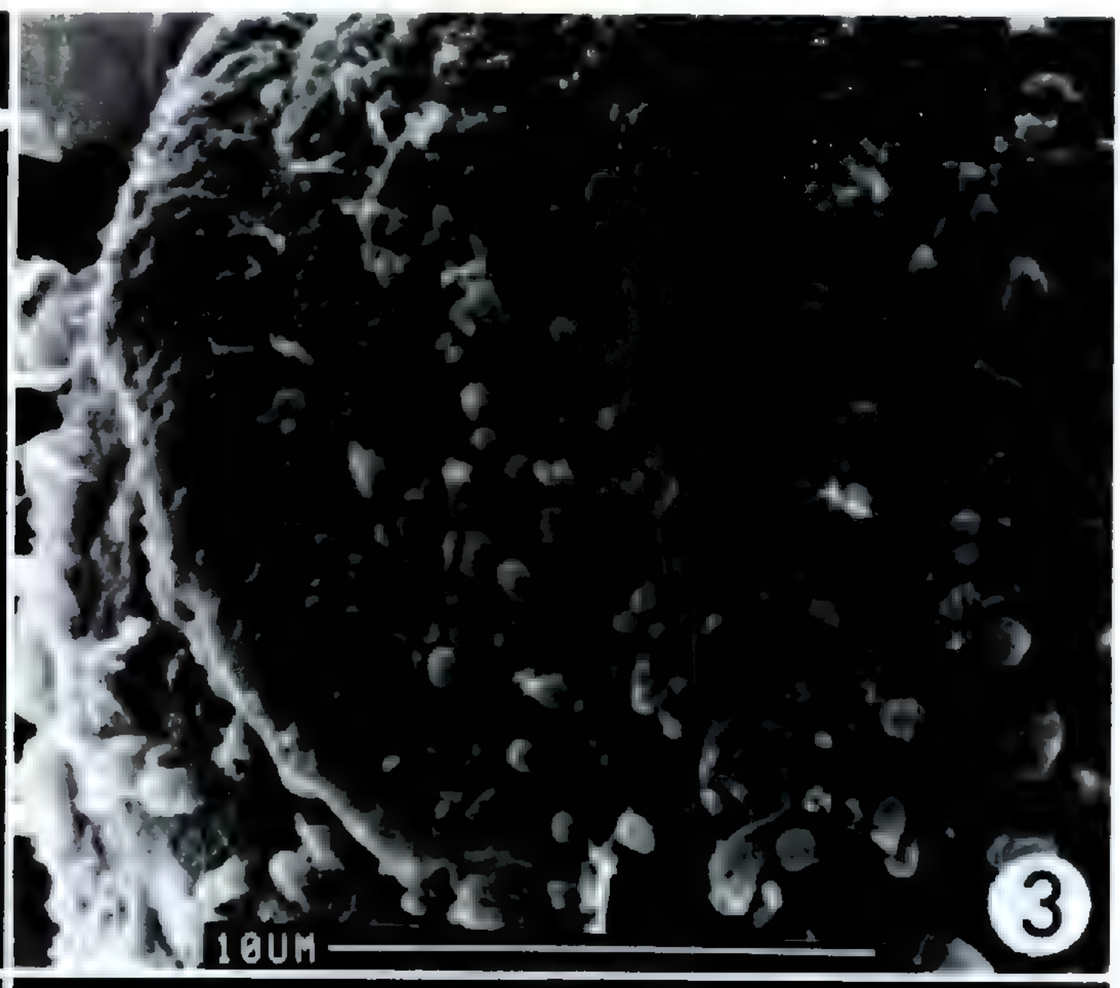
FIGURE 1. Expanded pollen grains of Ixioideae in polar and equatorial view (except for D), showing sulcus types.—A. *Anomatheca laxa*, monosulcate grain with double banded operculum.—B. *Ixia brevituba*, monosulcate grain with single banded operculum.—C. *Zygotritonia bongensis*, triaperturate grain, the apertures without opercula.—D. *Savannosiphon euryphylla*, omniaperturate grain. For dimensions of grains see Table 2.

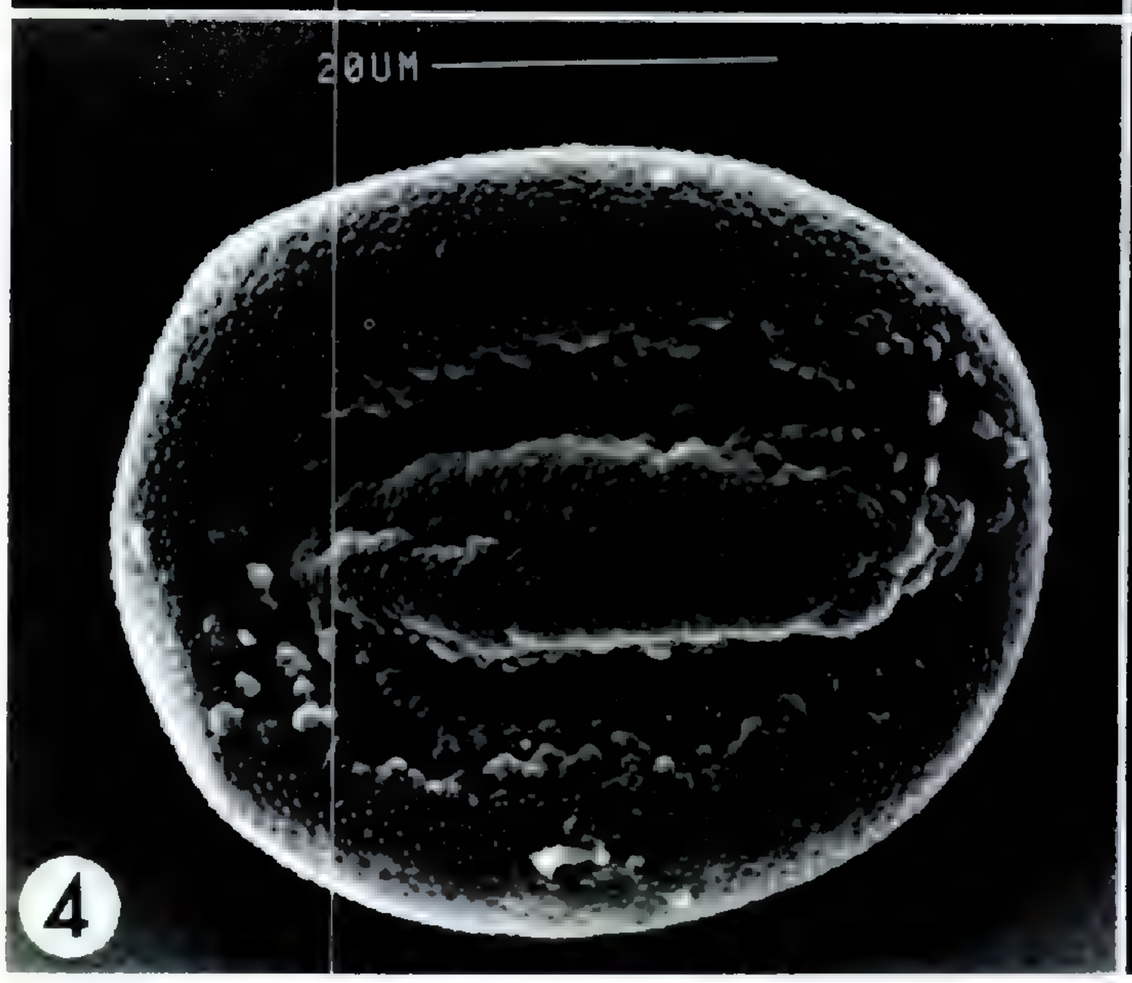
unusual members of the genus and are evidently taxonomically isolated from the other species of *Anomatheca* and the closely related *Freesia* (Goldblatt, 1972). The two species seem derived in the genus, *A. fistulosa* having a long perianth tube and flowers solitary on the branches, and *A. viridis* having a green perianth and autogamous reproduction. The possibility that these two species are united by the 1-banded operculum, or are misplaced in *Anomatheca*, should be considered in future studies of this genus. It seems reasonable to regard the 1-banded operculum in *A. fistulosa* and *A. viridis* as derived within the genus on the grounds explained above and because of their own specialized features.

The infrageneric variation in the opercular morphology in *Thereianthus* probably also has taxonomic significance. *Thereianthus juncifolius*, which has a 2-banded operculum, is isolated in the genus because of its lax inflorescence, but the possibility that it is misplaced is remote. The other species of *Thereianthus*, *T. racemosus*, which has a 2-banded operculum, may be primitive in the genus. It stands out morphologically in having small flowers with a short perianth tube (a plesiomorphic character in the genus). It should be considered less specialized than the long-tubed and often zygomorphic-flowered members of the genus, all of which have a 1-banded operculum. Thus, in this genus the hypothesis that the 2-banded operculum is the basic state also seems likely.

In the largely southern African genus *Romulea*







FIGURES 2–5. Sulcate pollen grains of Ixioideae.—2. *Pillansia templemannii* with 2-banded operculum.—3. Aperture detail in *P. templemannii*.—4. *Thereianthus minutus*, sulcate grain with 1-banded operculum with the median lacking exine.—5. *Lapeirousia neglecta*, sulcate grain showing operculum (one of the two bands has exfoliated) and scattered exine debris lying on the aperture membrane. Scale bar = 20 μm (2, 4, 5); = 10 μm (3).

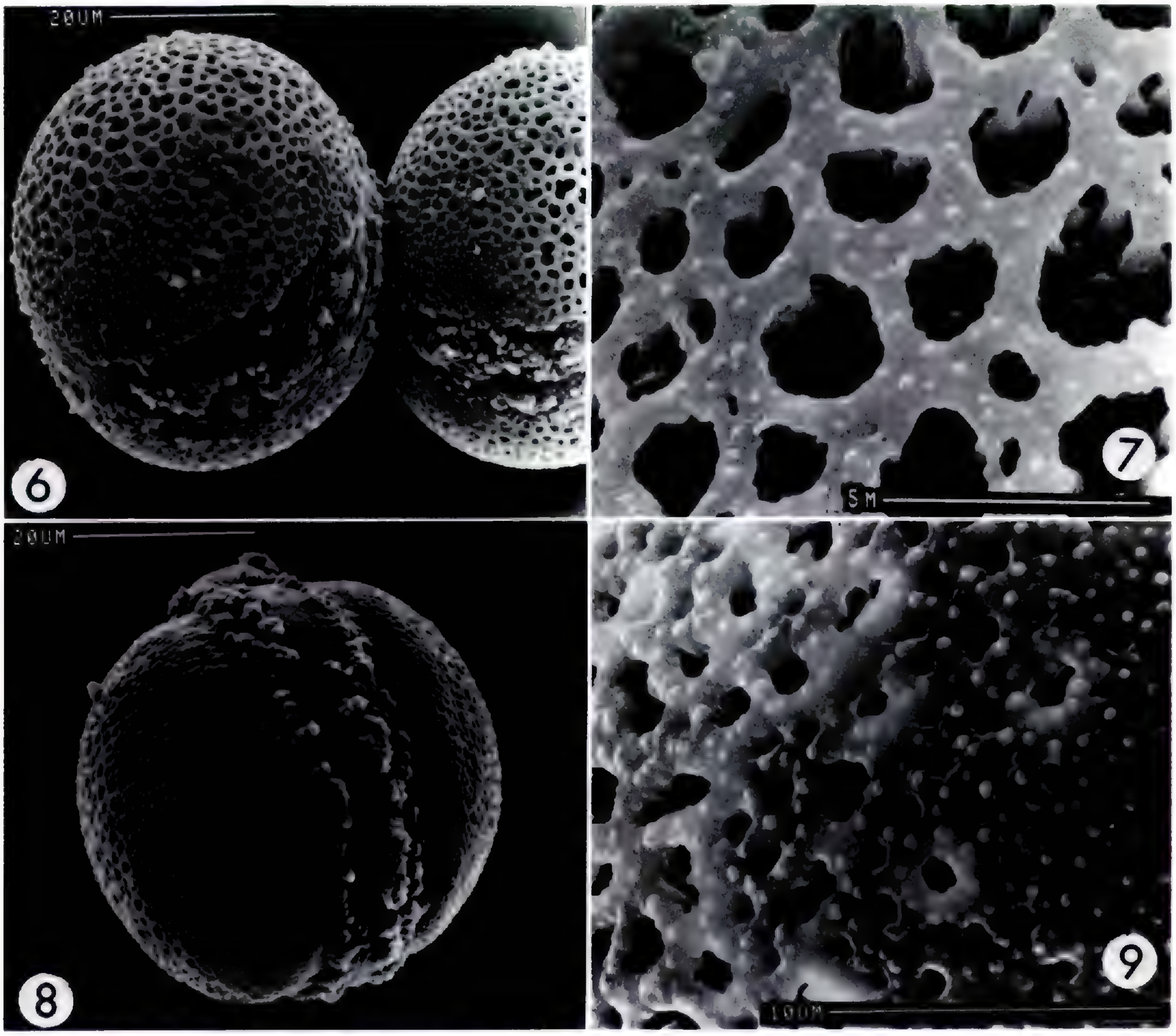
(whose close relatives are also southern African), only a few North African species are so far known to have a 1-banded or disorganized operculum, although pollen of few of the southern African species have been examined. A 1-banded operculum is thus presumably derived in the genus, but as far as we know there are no morphological or other reasons to view the species with a 1-banded operculum as specialized or derived from ancestors with a 2-banded operculum.

The only genus that seems consistently to have a 1-banded operculum is *Ixia*, and this is presumably an apomorphy for the genus. Lewis (1962) regarded *Ixia* as most closely related to *Dierama*. *Dierama*, which has a 2-banded operculum, is apparently less specialized in its evergreen habit but derived in its pendulous flowers and possibly also in its unusual leaf anatomy (Rudall & Goldblatt, in press; Goldblatt, in prep.).

SIGNIFICANCE OF THE ZONASULCATE APERTURE AND RETICULATE EXINE IN *MICRANTHUS*

Zonasulcate grains (previously described as syncolpate by Schulze, 1970) and a reticulate exine are almost certainly both apomorphic for *Micranthus*, evidently a fairly derived genus of Watsonieae (Goldblatt, 1989a).

Micranthus is undoubtedly correctly placed in Ixioideae despite its reticulate or largely reticulate exine, which corresponds to the patterning in other subfamilies of Iridaceae. In this connection, the transition from reticulate to microreticulate to perforate exine toward the sulcus margins, noted in preparation of *M. alopecuroides* and *M. tubulosus*, seems noteworthy. In Iridoideae with reticulate exine structure, perforate exine does not occur adjacent to the aperture (e.g., Goldblatt & Manning, 1989). The reticulate exine of *Micranthus* thus



FIGURES 6–9. Pollen grains and exine detail of *Micranthus*.—6. *M. alopecuroides*, whole grains showing exine fragments in the aperture.—7. *M. junceus*, detail of exine sculpture.—8. *M. tubulosus*.—9. Detail of transition from microreticulate to perforate exine in *M. tubulosus*. Scale bar = 20 μm (6, 8); = 5 μm (7); = 10 μm (9).

appears best regarded as a reversal to the basic state for the family.

Likewise, we consider the reticulate exine of *Thereianthus racemosus* a specialization for the species. The possibility that this character is shared with *Micranthus* must be seriously considered. The two genera are closely related (Goldblatt, 1989a), and the suggestion that they may be congeneric seems supported by this shared exine character. However, the unusual zonasulcate aperture of *Micranthus* seems to isolate it effectively from *Thereianthus*, despite their shared karyology, unusual leaf insertion, and similar corm, fruit, and seed morphology (Goldblatt, 1991).

The absence of intermediates between the sulcate-operculate and zonasulcate apertures in the subfamily makes exact interpretation of the aperture of *Micranthus* impossible. The aperture may have evolved through an extension of the sulcus around the grain through the distal pole and the loss of the operculum. Alternatively, the aperture may have been pushed into an equatorial position by the enlargement of the operculum to match the size of the other part of the exine (thus zonisulculate).

SIGNIFICANCE OF TRI-APERTURATE AND POLYRUGOIDATE GRAINS

The trisulcate grains of *Zygotritonia* are remarkable for Iridaceae and probably for the monocots. We speculate that the tri-aperturate condition may have evolved from an ancestor with a double-banded operculum by the enlargement of the opercular bands, and the displacement of the membrane areas away from the polar part of the grain toward the equator. *Zygotritonia* is a specialized genus (Goldblatt, 1989b) and must be derived from stock

that had a sulcus with a double-banded operculum. Whatever the phylogeny of this unusual aperture type, it is clear that *Zygotritonia* is additionally isolated in the subfamily by its specialized pollen grains.

The remarkable pollen grains of *Savannosiphon* reinforce our appreciation that the genus, segregated from *Lapeirousia* by Goldblatt & Marais (1979), is quite distinct from the palynologically uniform (as far as is known) *Lapeirousia*.

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SYSTEMATIC PLACEMENT OF THE PLATANACEAE IN THE HAMAMELIDAE[1]

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Abstract

A cladistic analysis of the basal Hamamelidae based upon 92 characters is presented. The results support a close phylogenetic relationship between the subfamily Altingioideae (Hamamelidaceae) and Platanaceae but suggest that present hypotheses concerning the derivation of the Hamamelidae from the Magnoliidae need revision. Analysis of the five subfamilies of Hamamelidaceae using Platanaceae as an outgroup yields a phylogeny that corresponds to the fossil record far better than does current theory. As a result of this study and recent paleobotanical and phytochemical evidence, it is suggested that Hamamelidae are at least as primitive as Magnoliidae.

Platanaceae are a monogeneric family of trees with a fossil history that extends to the Albian, Lower Cretaceous (Kutuzkina, 1974; Hickey & Doyle, 1977; Dilcher & Eriksen, 1983; Upchurch, 1984; Crane et al., 1986; Schwarzwalder, 1986). Cronquist (1981) considered Hamamelidales, which include Platanaceae, as an order of subclass Hamamelidae ancestral to all other orders within the subclass except the Trochodendrales. According to this view, Hamamelidales evolved from a Magnoliid or Magnoliid-derived taxon on a line of evolution that first spawned Trochodendrales. Recognition of Platanaceae as a well established angiosperm family in the Early Cretaceous raises questions concerning the current systematic placement of this family.

A diverse body of evidence supports a close systematic relationship between Platanaceae and Hamamelidaceae (Tippo, 1938; Jay, 1968; Takhtajan, 1969; Hickey & Wolfe, 1975; Cronquist, 1981; Zavada & Dilcher, 1986). Wolfe (1973) suggested a relationship between Platanaceae and Eupteleaceae based upon foliar characteristics.

Morphological similarities between Platanaceae and Hamamelidaceae—especially floral resemblances between hamamelidaceous subfamily Altingioideae and Platanaceae—strongly suggest alliance. However, there is no agreement concerning the relative advanced or primitive nature of the two families, and thus the extent of their relationship remains unresolved. Tippo (1938) felt that Platanaceae are "clearly more advanced than the Hamamelidaceae anatomically." Cronquist (1981) considered Platanaceae to have been derived earlier than Hamamelidaceae from a common stock of flowering plants. He commented that the flowers of Platanaceae are the more primitive of the two, but stated that "neither family can be derived from the other."

Procedures and Methods

A cladistic analysis of the basal Hamamelidae—Eupteleaceae, Platanaceae, and the five subfamilies of Hamamelidaceae—was conducted using Swofford's PAUP (Phylogenetic Analysis Using Parsimony) program (Swofford, 1984) on Indiana University's mainframe computer. PAUP options were chosen to consider all possible trees on the basis of maximum parsimony. Character state polarities were established by outgroup analysis using Tetracentraceae and Trochodendraceae as outgroups.

Ninety-two characters are presented for each of the nine taxa in Table 1. Character states are coded for presence or absence for each of the nine taxa surveyed. Presence of a character state in any species of a given family or subfamily resulted in that taxon being scored as positive for the trait. The data used in our analysis were gleaned from the literature or generated by Schwarzwalder (1986). The 92 characters include aspects of secondary chemical compounds, wood anatomy, epidermal characteristics, pollen structure, foliar morphology, petiole anatomy, seed structure, floral morphology and pollination adaptation, inflorescence type, and fruit type.

In our analysis the five subfamilies of the Hama-

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melidaceae, Altingioideae, Disanthoideae, Exbucklandioideae, Hamamelidoideae, and Rhodoleioideae, were treated as taxonomic equivalents to the Platanaceae, Eupteleaceae, Tetracentraceae, and Trochodendraceae. This subdivision was performed to insure a meaningful analysis of these taxa. The five subfamilies of the Hamamelidaceae are phenotypically quite distinct. Unlike the other families of the basal Hamamelidae, which display only minor genetic and phenotypic variation, the Hamamelidaceae, with 26 genera and more than 100 species (Cronquist, 1981), are extremely heterogeneous. If the family is analyzed as one taxon, the large degree of phenotypic variability encompassed by Hamamelidaceae tends to obscure intrafamilial and interfamilial relationships. Numerous authors have recognized the distinctness of the hamamelidaceous subfamilies and have recommended the elevation of one or more of them to familial status (Blume, 1928; Hayne, 1830; Lindley, 1836; Wilson, 1905; Nakai, 1943; Chang, 1959, 1964; Skvortsova, 1960; Willis, 1966; Takhtajan, 1969; Melikian, 1971, 1973a, b; Rao, 1974; Rao & Bhupal, 1974; Wolfe, 1973; Dahlgren, 1977; Jha, 1977).

These five subfamilies are considered as sister groups to Platanaceae and Eupteleaceae. Tetracentraceae and Trochodendraceae, together considered by Cronquist (1981) as members of the most primitive order within the Hamamelidae, were used as separate outgroups to establish character state polarities. Establishing character state polarities using the two families phenotypically closest to the Magnoliidae allows us to reconstruct Hamamelid evolution in relation to current evolutionary thought (Cronquist, 1981). By using Tetracentraceae and Trochodendraceae as outgroups we test the hypothesis of a Magnoliid-derived Hamamelidae. Cercidiphyllaceae and Myrothamnaceae are not considered in this analysis, because we feel that evidence suggests neither family as a hypothetical sister group to Platanaceae.

In order to determine the stability of relationships within the cladogram generated from this study, four test analyses were performed. In each test, 5% random error was introduced into the original data set, and PAUP was used to generate a cladogram(s). Using cladistics, one formulates the most direct course of evolution possible to hypothesize the evolutionary relationships of a given set of taxa. Evolutionary noise, i.e., homoplasy, occurs in a data set proportional to the extent that mosaic evolution occurs in a group of related taxa. Homoplasy is an expected component of any data set and tends to introduce ambiguity into cladistic results. The experimental addition of random error into this data set can be considered as extra homoplasy. Well-resolved relationships should be stable despite the addition of such evolutionary noise. Thus, this is a test of the stability of proposed relationships. Since cladistics formulates the evolutionary interrelationships of all taxa considered in an analysis, an error in the data set of one change in any taxon has ramifications for all taxa.

Rohlf & Sokal's (1981) statistical tables furnished random numbers. Three-digit random numbers were used to designate character states to be changed. The first digit of the number specified the taxon (1–9), and the last two digits specified the character (1–92). As all data are in presence-absence form rather than having three or more character states, characters could be reversed without ambiguity. Four tests of the initial cladogram (Fig. 1) were conducted. In each test 41 character states, 5% of the total 828 character states (92 characters for each of nine taxa), were reversed. A listing of the character states reversed in each of the four tests is presented in Table 2. Figure 2A–D illustrates the results of these tests. Consensus trees were calculated where more than one tree was determined to possess maximum parsimony. Swofford's CONTREE program, which uses the methods of Adams (1972) and Rohlf (1982), was used in these analyses.

Results and Discussion

The cladistic analysis resulted in one tree of a length of 157 steps (Fig. 1). In this cladogram, Platanaceae are placed within Hamamelidaceae sensu lato as a sister group to subfamily Altingioideae. Platanaceae and subfamily Altingioideae share 12 derived character states: the presence of cyanidin (character 5), glandular trichomes (character 17), actinodromous to palinactinodromous primary pattern of venation (character 42), the union of intercostal tertiary veins to secondaries (character 47), altingioid marginal venation (character 53), the presence of several vascular traces in petioles (characters 56 and 57), orthotropous ovules (character 60), small seeds (character 64), hard testas (character 69), minute petals (character 74), and nonperigynous flowers (character 83). The position of Eupteleaceae on the cladogram and the large synapomorphy list separating this family from Platanaceae and Hamamelidaceae suggest that Eupteleaceae and Platanaceae are more distantly related than is indicated by similarities of foliar features alone.

The cladogram suggests that Platanaceae orig-

TABLE 1. Characters and character states for A. Disanthoideae, B. Exbucklandioideae, C. Hamamelidoideae, D. Altingioideae, E. Rhodoleioideae, F. Platanaceae, G. Eupteleaceae, H. Tetracentraceae, I. Trochodendraceae. Superscripts: 1. Saupe (1981), 2. Seigler (1981), 3. Dahlgren et al. (1981), 4. Jay (1968), 5. Harborne (1967), 6. Gornall et al. (1979), 7. Metcalfe & Chalk (1965), 8. Tang (1943), 9. personal observation, 10. Bailey & Nast (1945), 11. Zavada & Dilcher (1986), 12. Praglowski (1974), 13. Bogle & Philbrick (1980), 14. Hickey & Wolfe (1975), 15. Wolfe (1973), 16. Nast & Bailey (1946), 17. Endress (1977), 18. Nast & Bailey (1945), 19. Boothroyd (1930), 20. Bogle (1970), 21. Rao (1974), 22. Schwarzwalder & Dilcher (1981), 23. Harms (1930). @ = not applicable; ? = unknown value.

	A	B	C	D	E	F	G	H	I
1. Cyanogens tyrosine-derived[1]	−	−	−	−	−	+	−	−	+
2. Monoterpenes iridoid[2,3]	−	−	−	+	−	−	−	−	−
3. Ellagic acid[3,4]	+	+	+	+	+	−	−	−	−
4. Myricetin[4,5]	−	+	+	+	+	+	−	−	+
5. Cyanidin[6]	−	−	−	+	?	+	−	−	−
6. Flavonols acylated[6]	−	−	−	−	−	+	−	−	−
7. Leucodelphinidine[4]	−	?	+	+	?	+	−	?	?
8. Leucocyanidine[4]	+	?	+	+	?	+	+	?	?
9. Vessels present[7,8]	+	+	+	+	+	+	+	−	−
10. Wood rays heterocellular[7]	+	+	+	+	+	−	+	+	+
11. Axial parenchyma banded[7]	−	−	+	−	−	+	−	−	+
12. Wood fiber length ≥ 1,600 μm[7]	+	+	+	+	+	+	−	+	+
13. Tyloses present[7]	−	−	+	+	−	+	+	@	@
14. Vessel elements > 800 μm[7,8]	+	+	+	+	+	−	+	@	@
15. Number bars/perforation plate > 20[7,8]	−	+	+	+	+	−	+	@	@
16. Perforation plates simple[7,8]	−	−	−	−	−	+	−	@	@
17. Trichomes glandular[7,9]	−	−	−	+	−	+	−	−	−
18. Trichomes stellate[7,9]	−	−	+	−	−	+	−	−	−
19. Trichomes branched[7,9]	−	−	−	−	−	+	−	−	−
20. Trichomes peltate[7]	−	+	−	−	−	−	−	−	−
21. Secretory cells[7,10]	+	+	+	+	+	−	+	+	+
22. Crystals solitary[7,10]	−	−	+	−	−	−	+	+	−
23. Crystals clustered[7,10]	−	+	−	+	+	+	−	+	−
24. Stomates laterocytic[7,10]	−	−	+	−	−	+	−	+	+
25. Stomates paracytic[9]	+	−	+	+	−	+	−	−	−
26. Stomates anomocytic[9]	−	−	−	−	−	+	+	−	−
27. Stomates cyclocytic[9]	−	+	−	−	+	−	−	−	−
28. Epidermis papillate[7]	−	−	+	−	+	−	+	−	−
29. Pollen tricolpate[11,12,13]	+	+	+	−	+	+	+	+	+
30. Pollen forate[11,12,13]	−	−	+	+	−	−	−	−	−
31. Pollen prolate[11,12,13]	+	+	+	−	+	+	+	+	+
32. Pollen spherical[11,12,13]	+	+	+	+	−	+	+	−	+
33. Pollen oblate[11,12,13]	−	−	+	−	−	−	+	−	+
34. Endexine present[11,12]	+	−	+	+	−	+	+	+	+
35. Endexine thick at aperture[11,12]	+	−	−	−	+	−	+	+	+
36. Endexine not through aperture[11,12]	−	−	+	+	−	+	−	−	−
37. Pollen psilate[11,12,13]	+	+	+	−	+	+	−	+	+
38. Pollen scabrate[11,12,13]	−	−	−	−	−	−	+	−	−
39. Pollen rugulate[11,12,13]	−	+	+	+	−	−	−	−	−
40. Leaves opposite[7,9]	−	−	+	−	−	−	−	−	−
41. Primary veins pinnate[9,14]	−	−	+	+	+	+	+	−	+
42. Primary veins (palin)actinodromous[9,14]	−	−	−	+	−	+	−	+	−
43. Primary veins acrodromous[9,14]	+	+	−	−	−	−	−	−	−
44. Secondary veins craspedodromous[9,14,15]	−	−	+	+	−	+	+	−	−
45. Secondary veins camptodromous[9,14,15]	+	+	−	+	+	+	−	+	+
46. Tertiary veins strongly percurrent[9]	−	−	+	−	−	+	+	−	−
47. Intercostal tertiaries joining secondaries[9]	−	−	−	+	−	+	+	−	−
48. Tertiary veins forming chevrons[9]	+	+	+	+	+	+	+	+	−
49. Teeth chloranthoid[9,14]	−	−	−	−	−	−	−	+	+

TABLE 1. Continued.

	A	B	C	D	E	F	G	H	I
50. Teeth platanoid[9,14]	−	−	−	−	−	+	+	−	−
51. Secondary veins decurrent[9,14]	−	−	−	−	+	−	−	−	+
52. Teeth admedially oriented[9,14]	−	−	−	+	−	−	−	−	−
53. Altingioid marginal venation[9]	−	−	−	+	−	+	−	−	−
54. Teeth hamamelidoid[9]	−	−	+	−	−	−	−	−	−
55. Nodes unilacunar[7,16]	−	−	−	−	−	−	+	−	−
56. Number petiole traces = 1[7,16]	+	+	+	−	+	−	−	+	+
57. Number petiole traces > 1[7,16]	−	−	−	+	−	+	+	−	+
58. Petiole encloses axillary bud[7,9,10]	−	−	−	−	−	+	−	+	−
59. Stipules present[7,17]	+	+	+	+	+	+	−	+	−
60. Ovules anatropous[16,18,19,20]	+	+	+	−	+	−	+	+	+
61. Embryo narrow[21]	+	+	+	+	+	+	−	−	−
62. Raphe bundle enclosed[18,21]	−	−	−	−	−	−	−	+	+
63. Embryo minute[16,18,21]	−	−	−	−	−	−	+	+	+
64. Seeds small[16 18,21]	−	−	−	+	−	+	+	+	+
65. Subchalazal area vascularized[16,18,21]	−	−	−	−	−	−	−	+	+
66. Tegmen two-layered[21]	−	−	−	−	−	−	−	+	+
67. Tegmen persistent in mature seed[21]	+	+	+	+	+	−	−	+	+
68. Raphe bundle ending at chalaza[18,21]	+	+	+	+	+	+	−	−	−
69. Testa hard, conspicuous[16,21]	+	+	+	−	+	−	−	−	−
70. Carpels fused[16,18,19,20]	+	+	+	+	+	−	−	−	+
71. Carpel wall open[16,18,19,20]	−	−	−	−	−	+	−	+	+
72. Flowers imperfect[16,18,19,20]	−	+	+	+	−	+	−	−	−
73. Flowers perfect[16,18,19,20]	+	−	+	−	+	−	+	+	+
74. Petals minute or absent[16,18,19,20,22]	−	−	−	+	−	+	+	+	+
75. Sepals minute or absent[16,18,19,20,22]	−	+	−	+	−	+	+	−	+
76. Carpels sessile[16,18,19,20]	+	+	+	+	+	+	−	+	+
77. Stamens valvate[16,17,18,19,20]	−	−	+	−	−	−	−	−	−
78. Ovules > 1[16,17,19,20]	−	−	+	−	−	+	−	−	−
79. Anemophilous[16,17,18]	−	+	+	+	−	+	+	+	+
80. Entomophilous[16,17,18]	+	−	+	−	+	−	+	−	+
81. Epigynous[16,13,19,20,23]	−	−	+	+	−	−	−	−	−
82. Hypogynous[16,18,19,20,23]	+	−	+	−	−	+	+	+	+
83. Perigynous[16,18,19,20,23]	−	+	+	−	+	−	−	−	−
84. Flowers solitary or in pairs[16,17,18,19,20]	+	−	+	−	−	−	+	−	−
85. Flowers in spikes[16,17,18,19,20]	−	−	+	−	−	−	−	+	−
86. Inflorescence a cyme or cymose raceme[16,17,18,19,20]	−	−	+	+	−	−	−	−	+
87. Flowers in heads[16,17,18,19,20]	−	+	+	+	−	+	−	−	−
88. Flowers in pseudanthia[16,17,18,19,20,21]	−	−	−	−	+	−	−	−	−
89. Fruit a follicle or follicetum[16,17,18,19,20,21]	−	−	−	−	−	−	−	+	+
90. Fruit capsular[16,17,18,19,20,21]	+	+	+	+	+	−	−	−	−
91. Fruit an achene[16,17,18,19,20,21]	−	−	−	−	−	+	−	−	−
92. Fruit a samara[16,17,18,19,20,21]	−	−	−	−	−	−	+	−	−

inated late in a series of evolutionary events that gave rise to the subfamilies of Hamamelidaceae. The position of Disanthoideae in the cladogram is corroborated by Cronquist (1968, 1981) and Takhtajan (1969); however, this is not unexpected since their placement of Disanthoideae is based upon their similarity to the Magnoliidae. However, the positions of Hamamelidoideae, Altingioideae, and Platanaceae as the most recently derived taxa of the group do not agree with the fossil record. Members of the Platanaceae are first known from fossil leaves and reproductive material from the Albian, Lower Cretaceous (Kutuzkina, 1974; Hickey & Doyle, 1977; Dilcher & Eriksen, 1983; Upchurch, 1984; Crane et al., 1986; Schwarzwalder, 1986). The first megafossil records of Altingioideae are leaves from the genus *Liquidambar* L. in the Cenomanian, lowermost Upper Cretaceous, (Newberry, 1898; Chesters et al., 1967) and Upper Cretaceous (Brown, 1933; En-

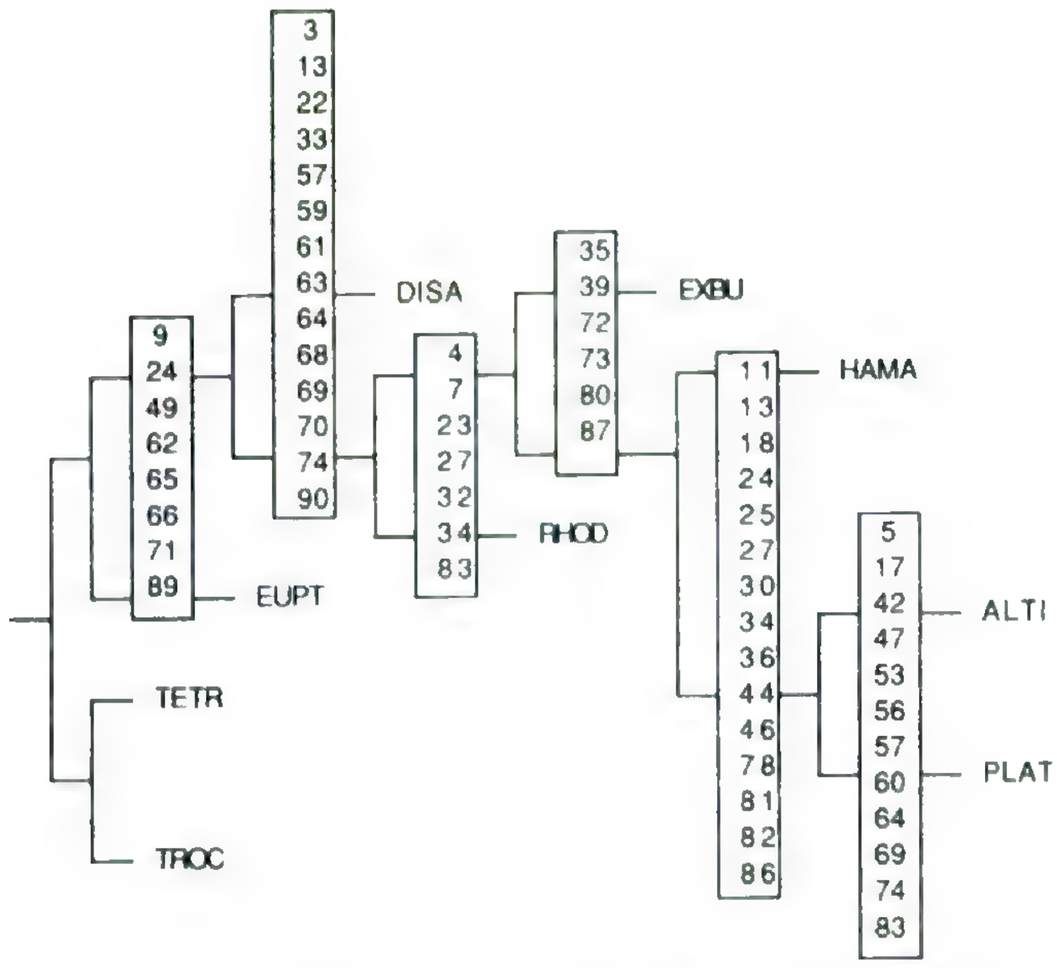

FIGURE 1. Cladogram of the basal Hamamelidae with Tetracentraceae and Trochodendraceae as outgroups. Synapomorphies are designated by rectangles. Numbers in rectangles make reference to character numbers in Table 1. Abbreviations above are as follows: TETR = Tetracentraceae, TROC = Trochodendraceae, EUPT = Eupteleaceae, DISA = Disanthoideae, RHOD = Rhodoleioideae, EXBU = Exbucklandioideae, HAMA = Hamamelidoideae, ALTI = Altingioideae, and PLAT = Platanaceae.

dress in Cronquist, 1981). The first records of megafossils from the Hamamelidoideae are foliar fossils from the lower Paleocene (Mathiesen, 1932; Hollick, 1936; Koch, 1963; Wolfe, 1966, 1973). The early fossil records of these putatively advanced taxa and the lack of early fossil representation of the other taxa in the cladogram suggest that the analysis may not be valid.

The discrepancy between these results and the fossil record prompted us to test the validity of our initial analysis. Four tests were performed by introducing 5% error into the data set and conducting cladistic analyses on each with the PAUP software. Results are presented in Figure 2.

The relationship between Altingioideae and Platanaceae, and the position of Eupteleaceae are preserved in the four consensus trees in Figure 2. The other subfamilies of Hamamelidaceae, however, are subject to extensive rearrangement with the addition of random error. Thus, the phylogenetic reconstruction of the basal Hamamelidae presented in Figure 1 is questionable if we assume that there is at least 5% homoplasy in the origina! data set.

A possible source of error in the hypothetical phylogeny presented in Figure 1 is the use of the two families of Trochodendrales as outgroups in the cladistic analysis. Fossil evidence of Platanaceae in the Albian, upper Lower Cretaceous (Kutuzkina, 1974; Hickey & Doyle, 1977; Dilcher & Eriksen, 1983; Upchurch, 1984; Crane et al., 1986; Schwarzwalder, 1986), predates the occurrence of any other member of the Hamamelidae. Hickey & Wolfe (1975) noted the early occurrence of the platanoids and suggested them as "possible early members of the trend toward the hamamelid line." If we assume that their early occurrence and morphological similarity to other members of

TABLE 2. Character state reversals for the tests of cladistic relationships in the basal Hamamelidae. Character state reversals are identified, by taxon, for each of the four tests presented in the body of the paper. Numbers given after each taxon correspond to the characters listed in Table 1.

Random Error Test One (Fig. 2A)

Disanthoideae: 29, 33, 34, 54, 70, 89
Exbucklandioideae: 30, 38, 60, 80
Hamamelidoideae: 4, 14, 23, 27, 38, 57
Altingioideae: 68, 75
Rhodoleioideae: 2, 4, 23, 27, 31, 48, 52, 69, 82, 86
Platanaceae: 5, 76, 85
Eupteleaceae: 23, 56, 59, 64, 68, 71
Tetracentraceae: 59, 61, 76
Trochodendraceae: 65

Random Error Test Two (Fig. 2B)

Disanthoideae: 30, 49, 71, 88
Exbucklandioideae: 25, 34
Hamamelidoideae: 23, 45, 52, 91
Altingioideae: 5, 15, 18, 20, 45, 51, 54, 86
Rhodoleioideae: 20
Platanaceae: 5, 59, 66, 78
Eupteleaceae: 16, 28, 43, 44, 46, 84, 89
Tetracentraceae: 18, 32, 42, 67, 73
Trochodendraceae: 1, 27, 40, 55, 64, 73

Random Error Test Three (Fig. 2C)

Disanthoideae: 3, 31, 38, 59
Exbucklandioideae: 4, 19, 53
Hamamelidoideae: 18, 22, 34, 61, 77, 79
Altingioideae: 48, 52, 70, 80, 86, 91
Rhodoleioideae: 16, 18, 30, 43, 48, 52, 59, 76
Platanaceae: 5, 33, 52
Eupteleaceae: 32, 43, 66, 68
Tetracentraceae: 81, 91
Trochodendraceae: 19, 34, 56, 63, 69

Random Error Test Four (Fig. 2D)

Disanthoideae: 7, 75, 77, 84, 87, 92
Exbucklandioideae: 4, 6, 39, 50
Hamamelidoideae: 3, 39, 78
Altingioideae: 10, 73, 88
Rhodoleioideae: 19, 58, 60, 65, 68, 71, 81
Platanaceae: 26, 28, 37, 62
Eupteleaceae: 23, 24, 54, 91
Tetracentraceae: 4, 12, 24, 25, 48, 66, 67, 81
Trochodendraceae: 40, 55

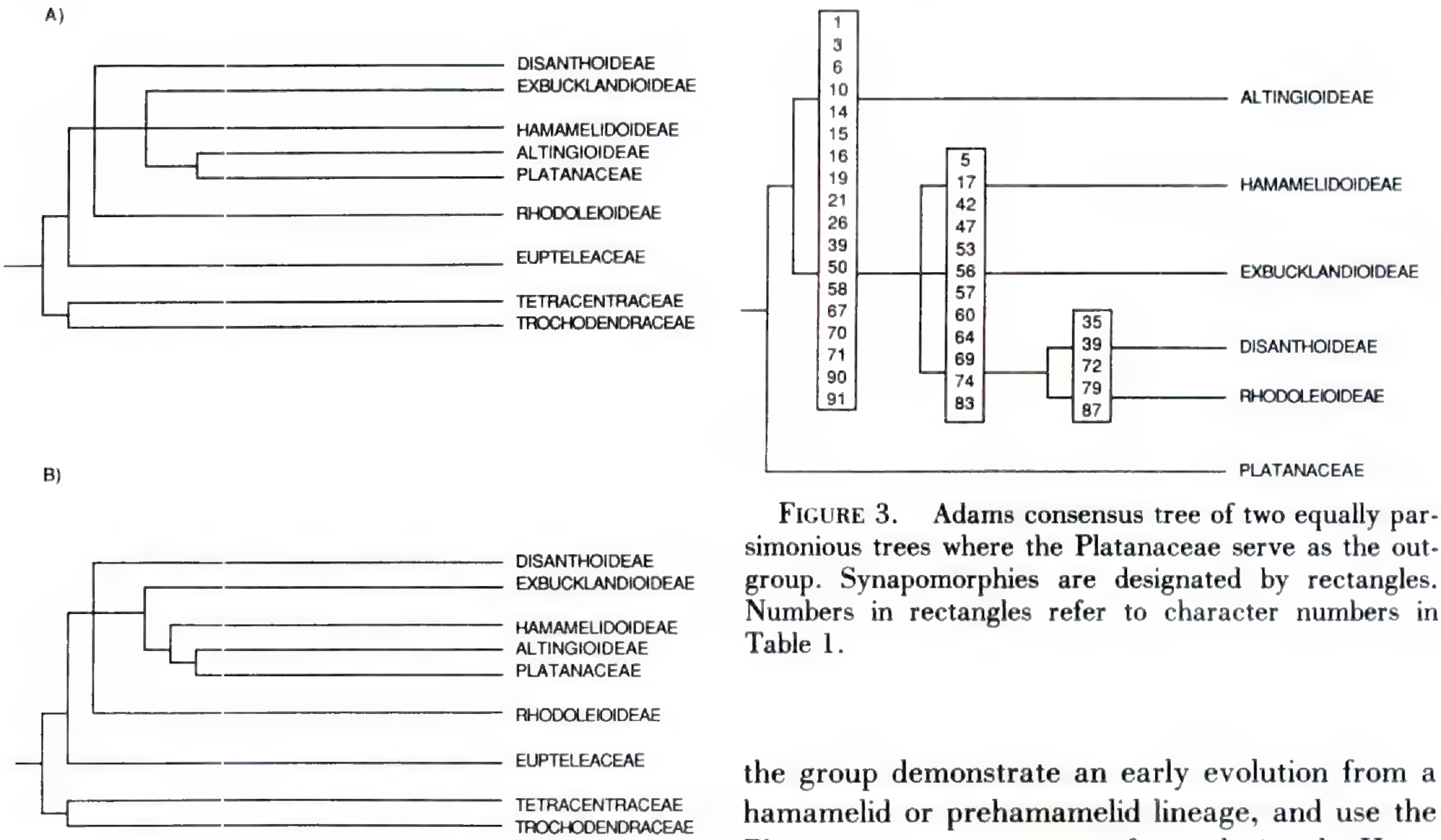

FIGURE 3. Adams consensus tree of two equally parsimonious trees where the Platanaceae serve as the outgroup. Synapomorphies are designated by rectangles. Numbers in rectangles refer to character numbers in Table 1.

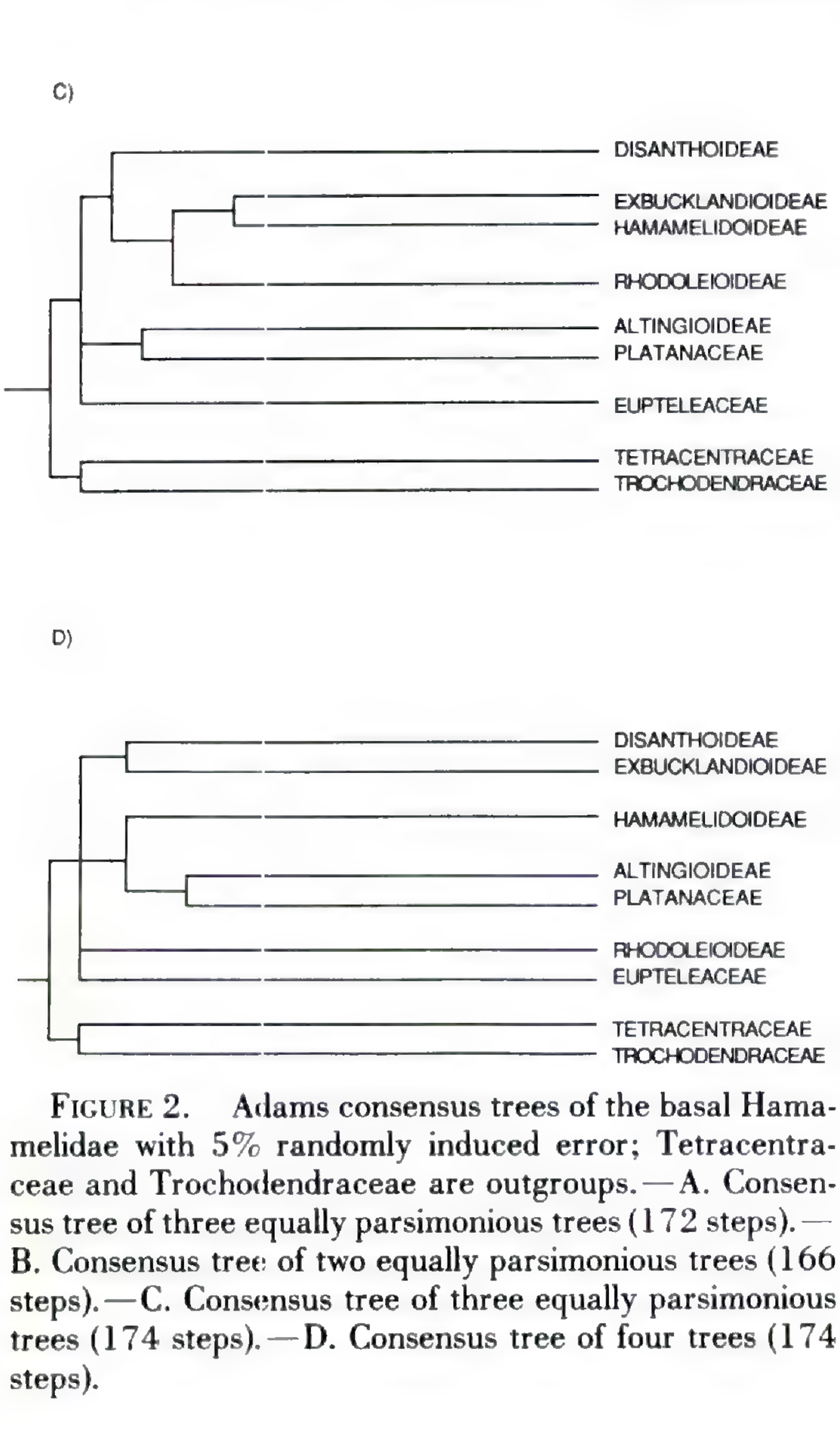

FIGURE 2. Adams consensus trees of the basal Hamamelidae with 5% randomly induced error; Tetracentraceae and Trochodendraceae are outgroups.—A. Consensus tree of three equally parsimonious trees (172 steps).—B. Consensus tree of two equally parsimonious trees (166 steps).—C. Consensus tree of three equally parsimonious trees (174 steps).—D. Consensus tree of four trees (174 steps).

the group demonstrate an early evolution from a hamamelid or prehamamelid lineage, and use the Platanaceae as an outgroup for analyzing the Hamamelidaceae, we obtain an alternative hypothesis of evolution in these two families (Fig. 3).

Figure 3 suggests that Altingioideae were the earliest-derived of the hamamelidaceous subfamilies. Later evolution in the family, according to the analysis, resulted in the evolution of the other four subfamilies with Disanthoideae and Rhodoleioideae being the latest-derived. While the consensus tree (Fig. 3) demonstrates the difficulty in resolving the node connecting Hamamelidoideae, Exbucklandioideae, and the Disanthoideae–Rhodoleioideae group, there is support for some of the relationships proposed by this cladogram. The position of Altingioideae as the earliest-derived subfamily of Hamamelidaceae is supported by 12 synapomorphies, which include features of phytochemistry, epidermal anatomy, venation, petiole anatomy, ovule and seed morphology, and floral structure (Fig. 3).

There is corroborative evidence from the fossil record for this phylogenetic scheme (Fig. 3). As mentioned previously, Platanaceae can be traced to the Lower Cretaceous, Altingioideae to the Upper Cretaceous, and Hamamelidoideae to the Lower Paleocene. Foliar megafossil records of Exbucklandioideae date from the Upper Oligocene (Lakhanpal, 1958) and Lower Miocene of Oregon (Brown, 1946) and the Middle Miocene of Washington State (Brown, 1946). We could find no records of fossil leaves, flowers, or fruits of the Disanthoideae or Rhodoleioideae. However, Tiffney (1986) reviewed records of dispersed seeds of *Rhodoleia* Champ. from the Upper Eocene (Mai & Walther, 1985) and *Disanthus* Maxim. from the

Lower Oligocene (Mai & Walther, 1978). These data suggest that Platanaceae may have been the earliest offshoot of a lineage that later gave rise to Altingioideae and, still later, Hamamelidoideae and other subfamilies of the Hamamelidaceae.

Hickey & Wolfe's (1975) suggestion that "Cercidiphyllales" and Trochodendrales form a clade separate from the remainder of the subclass that was derived from a prehamamelid or hamamelid lineage is in need of elaboration. Although our data suggest that the Eupteleaceae might be better placed in the Trochodendrales than the Hamamelidales, they lend some support for the derivation of the Hamamelidales from the "platanoids" proposed by Hickey & Wolfe (1975). The early occurrence of Platanaceae along with their cladistic proximity to Altingioideae and distance from Trochodendrales does not support inclusion of Trochodendrales in the lineage that led directly to the evolution of Platanaceae and Hamamelidaceae.

The cladistic analysis of the Hamamelidaceae using the Platanaceae as an outgroup results in a cladogram that differs drastically from current conceptions of evolution in the family (Cronquist 1968, 1981; Takhtajan, 1969) but agrees overall with the fossil record. We are not suggesting that this reconstruction represents the one true phylogeny of Platanaceae and Hamamelidaceae. Yet, we propose that the current practice of rooting the Hamamelidae in the Magnoliidae is in need of reevaluation. Paleobotanical (Dilcher, 1979; Retallack & Dilcher, 1981) and phytochemical data (Giannasi, 1986) suggest that Hamamelidae are at least as primitive as Magnoliidae. Examination of the Hamamelidae without assumptions as to their presumed ancestors may facilitate our understanding of the subclass and of angiosperm evolution.

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ANALISIS MULTIVARIADO DEL COMPLEJO DE TRES ESPECIES DE *BRUNELLIA* (BRUNELLIACEAE)[1]

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Resumen

Análisis de agrupamiento de componentes principales (ACP) y el árbol del valor mínimo (PRIM) fueron usados para esclarecer la sistemática de tres taxa de *Brunellia: B. antioquensis* (Cuatrec.) Cuatrec., *B. comocladifolia* Humb. & Bonpl., y *B. sibundoya* Cuatrec. Fue tambien estudiada la validez de las subespecies para los dos últimos taxa. Diez y siete Unidades Taxonómicas Operacionales (UTO) representaron los taxa, y se muestrearon 32 caracteres morfológicos para cada UTO. Con base en la similitud total de los 32 caracteres se reconocen dos especies, *B. comocladifolia* y *B. sibundoya*, y cuatro subespecies de las seis consideradas al iniciar el trabajo. Las dos especies se encuentran a diferentes niveles altitudinales; la temperatura relacionada directamente con el gradiente altitudinal es posiblemente el factor importante en la diferenciación específica. A nivel específico los caracteres diagnósticos se refieren al número de estípulas, al indumento de los folículos y a la forma de la semilla. Los caracteres diagnósticos para el reconocimiento a nivel infraespecífico tienen que ver con el número de lobulos del cáliz y el número de carpelos; la humedad es posiblemente el factor de mayor importancia en la variación floral. Los resultados del análisis fenético muestran que *B. antioquensis* corresponde a una subespecie de *B. sibundoya*, y los taxa infraespecíficos *B. comocladifolia* subsp. *boyacencis* y *B. sibundoya* subsp. *sebastopola* son sinónimos de *B. comocladifolia* subsp. *cundinamarcensis* y *B. sibundoya* subsp. *sibundoya*, respectivamente. El estudio de la estructura de la exina bajo el microscopio de barrido permite tambien reconocer la variación infraespecífica. Se identifican cuatro áreas o microáreas geográficas correlacionadas con cuatro diferentes combinaciones de caracteres y que corresponden a la distribución geográfica para Colombia de los cuatro taxa infraespecíficos reconocidos bajo este estudio. El número cromosómico, $2n = 28$, es reportado por primera vez para *B. comocladifolia* subsp. *cundinamarcensis* y *B. sibundoya* subsp. *sibundoya*.

Abstract

Clustering analysis, Principal Component Analysis (PCA), and Minimum Spanning Tree (PRIM) were used to define three taxa of *Brunellia: B. antioquensis* (Cuatrec.) Cuatrec., *B. comocladifolia* Humb. & Bonpl., and *B. sibundoya* Cuatrec. The subspecies were studied also. Seventeen OTUs represented the three taxa, and 32 morphological characters were sampled for all OTUs. Two species, *B. comocladifolia* and *B. sibundoya*, and four subspecies instead of six were recognized. The two species are localized at different elevations. Diagnostic characters at the specific level are related to the seed shape, indumentum of follicles and stipule number. The infraspecific variation is related to the number of lobules of the calyx and the number of carpels and is associated with variation in humidity. As a result of the phenetic study, *B. antioquensis* is considered a subspecies of *B. sibundoya*; *B. comocladifolia* subsp. *boyacensis* is a synonym of subsp. *cundinamarcensis*; and *B. sibundoya* subsp. *sebastopola* is synonymous with *B. sibundoya* subsp. *sibundoya*. The pollen structure of the exine, studied using a scanning electron microscope (SEM), shows infraspecific variation also. The subspecies are found in different geographic areas, and these areas are correlated with four different character combinations. The chromosome number, $2n = 28$, is reported for the first time for *B. comocladifolia* Humb. & Bonpl. subsp. *cundinamarcensis* Cuatrec. and *B. sibundoya* Cuatrec. subsp. *sibundoya*.

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Brunellia Humb. & Bonpl. es el único género de la familia Brunelliaceae, completamente neotropical y con una amplia distribución y especiación en los bosques Andinos de Colombia. En el estado actual del conocimiento de la familia, el género comprende dos secciones y trece subsecciones (Cuatrecasas, 1970, 1985). De las 60 especies registradas actualmente para el neotrópico, 39 han sido reportadas para Colombia (Cuatrecasas, 1970, 1985; Orozco 1981, 1985, 1986).

En la revisión que se adelanta para Brunelliaceae se encontró un complejo de tres especies muy semejantes morfológicamente con superposición e inconsistencia de caracteres. Los tres taxa se encuentran ubicados en la sección *Brunellia* Cuatrec. subsección *Comocladifoliae* Cuatrec. La subsección esta definida por la presencia de hojas opuestas e imparipinadas, folíolos con 10–17 pares de nervios secundarios, margen doble o simple, dentada, con indumento patulo. Las flores son pequeñas, y el caliz de 2.5–7.0 mm en diámetro con 4–6 piezas. El endocarpo es cartilaginoso en formo de U, y el exocarpo de pelos derechos y rígidos.

El actual estudio tuvo como objetivos: establecer los límites de variación y la validez de los tres taxa conocidos como *Brunellia antioquensis* (Cuatrec.) Cuatrec., *Brunellia comocladifolia* Humb. & Bonpl., y *Brunellia sibundoya* Cuatrec.; y esclarecer la existencia de subespecies cuya limitación geográfica para algunas de ellas discrepa del concepto clásico de subespecie Mayr (1963). Otro de los objetivos consistió en el estudio de caracteres no revisados anteriormente, tales como polen y cromosomas, con el propósito de conocer su utilidad y aplicación en la sistemática de la familia. Por otra parte, con este estudio se pretende aclarar los problemas encontrados por Cuatrecasas (1985) en cuanto a la determinación de las poblaciones de *B. comocladifolia* y *B. sibundoya*, y provenientes de Cundinamarca, señalando entre ellas una posible hibridación.

Problemas similares a los planteados en este trabajo han sido resueltos por medio del análisis multivariado, el cual permite un conocimiento mas exacto de los caracteres.

Materiales y Métodos

Muestras de *Brunellia antioquensis*, *Brunellia comocladifolia*, y *Brunellia sibundoya* fueron coleccionadas en la región Andina colombiana, tratando de cubrir la mayor parte de ella para registrar el rango total geográfico de distribución y la variación completa de las especies. El material fue determinado con base en las claves, en la distribución geográfica, y las colecciones preexistentes en los herbarios de COL, VALLE, y MEDEL determinadas por Cuatrecasas.

En la elección de las 17 Unidades Taxonómicas Operacionales (Tabla 1) se tuvo en cuenta que las mismas representaran la variación total de los taxa y cada UTO exhibiera el estado adulto de desarrollo (en fruto). Para algunos casos las UTO están conformadas por varias muestras de un individuo y para otros casos muestras de dos o mas colecciones de varios individuos presentes en un mismo sitio. Esta última consideración fue hecha por la variación sexual exhibida en estos taxa.

Un total de 32 caracteres morfológicos florales y vegetativos fueron registrados para cada UTO (Tabla 2) de los cuales 24 son cuantitativos continuos, 3 cuantitativos discontinuos (caracteres 5, 6, y 8), 2 cualitativos doble estado (caracteres 16 y 23) y 3 cualitativos multiestado (caracteres 30, 31, y 32). Varios de estos caracteres habian sido usados como diagnósticos, otros fueron elegidos teniendo en cuenta si el estado del caracter difería por lo menos en una UTO. Los caracteres de consistencia del folíolo, forma y base del folíolo, y número de nervios secundarios utilizados en previos trabajos para diferenciar los taxa, no fueron tenidos en cuenta en este estudio por la dificultad en definir con exactitud, para el caso del primer caracter, los estados coriáceo-subcoriáceo o cartáceo de moderadamente coriáceo; para el segundo y tercer caracter debido a la variabilidad intra-UTO; y para el cuarto por la ausencia de variación entre las UTO. Los caracteres cualitativos multiestados fueron codificados con base al razonamiento de una secuencia lógica de variación del caracter. Para los caracteres cuantitativos continuos el valor promedio fue anotado directamente.

La matriz básica de datos (Apéndice 1) fue sometida a distintos análisis multivariados utilizando el programa NT-SYS de Rohlf et al. (1971). Dos análisis de agrupamiento, a partir de una matriz de similitud de distancia y de una matriz de correlación; un análisis de ordenamiento (ACP); el analisis del árbol de la mínima distancia (PRIM); y los arboles de consenso fueron los análisis practicados en este trabajo (Fig. 1). En los análisis de agrupamiento, para el cálculo de la matriz de distancia, se usó el coeficiente taxonómico (TD) de Sokal (1961) y para el de la matriz de correlación el momento producto de Pearson. Las técnicas de agrupamiento del método de grupo par (Sneath & Sokal, 1973), ligamiento promedio ponderado (WPMGA), ligamiento completo (LC), y ligamiento promedio no ponderado (UPMGA) fueron utilizadas

TABLA 1. Relación de las UTO con sus respectivas determinaciones y referencias. Material de origen para los análisis de polen B y de cromosomas C. Cada UTO fue coleccionada en Colombia.

UTO 1 *Brunellia comocladifolia* subsp. *comocladifolia*. Valle del Cauca, Municipio de Dagua, Pichendé, 1,650 m, *Orozco, Lozano & Vidal 1156* (COL) (6 especímenes).

UTO 2 *Brunellia comocladifolia* subsp. *comocladifolia*. Cauca, Municipio de Popayán, Piendamó, 1,800 m, *Orozco, Vidal & Lozano 1160* (COL), B (5 especímenes).

UTO 3 *Brunellia comocladifolia* subsp. *comocladifolia*. Valle del Cauca, Municipio, Jamundí, Villa Colombia, 1,700 m, *Orozco, Vidal & Lozano 1228* (COL) (3 especímenes).

UTO 4 *Brunellia comocladifolia* subsp. *cundinamarcensis* Cundinamarca, Municipio de Yacopí, 1,730 m, *Orozco, Franco & Lozano 1105* (COL), B, C (7 especímenes).

UTO 5 *Brunellia comocladifolia* subsp. *cundinamarcensis*. Cundinamarca, Municipio de La Palma, 1,680 m, *Orozco, Franco & Lozano 1102* (COL), B (8 especímenes).

UTO 6 *Brunellia comocladifolia* subsp. *boyacensis*. Boyacá, Municipio de La Victoria, Alto del Chapón, 1,800 m, *Orozco, Sanabria & Sanchez 1258* (COL), C; departamento de Boyacá, Muncipio La Victoria hacia Quípama, 1,350 m, *Orozco, Sanabria & Sanchez 1267* (COL), B (11 especímenes).

UTO 7 *Brunellia sibundoya* subsp. *sibundoya*. Putumayo Valle de Sibundoy, 1,650 m, *Orozco, Lozano & Vidal 1200, 1203* (COL); 1,650 m, *Bristol 1247* (COL); 2,000 m, *Schultes 3202* (COL) (7 especímenes).

UTO 8 *Brunellia sibundoya* subsp. *sibundoya*. Cauca, Municipio del Puracé, Moscopán, 2,230 m, *Orozco, Lozano & Vidal 1162* (COL) (3 especímenes).

UTO 9 *Brunellia sibundoya* subsp. *sibundoya*. Cauca, Municipio del Tambo, 2,300 m, *Orozco, Vidal & Lozano 1173* (COL), B (6 especímenes).

UTO 10 *Brunellia sibundoya* subsp. *sibundoya*. Valle del Cauca, Municipio de Tulua, Barragán, 2,250 m, *Orozco, Vidal & Lozano 1120* (COL) (6 especímenes).

UTO 11 *Brunellia sibundoya* subsp. *sebastopola*. Cundinamarca, Municipio de Bojacá, 2,550 m, *Orozco, Lozano & Franco 1091, 1092, 1093* (COL), B (17 especímenes).

UTO 12 *Brunellia sibundoya* subsp. *sebastopola*. Cundinamarca, Municipio de San Francisco Sabaneta, 2,500 m, *Orozco, Franco, Lozano & Barrera 1098* (COL), C (6 especímenes).

UTO 13 *Brunellia sibundoya* subsp. *sebastopola*. Cundinamarca, Municipio de Zipacón, Estación de Sebastopol, 2,480 m, *Orozco & Carbonó 1271, 1272, 1273* (COL) (13 especímenes).

UTO 14 *Brunellia antioquensis*. Antioquia, Municipio de Medellín, Cerro del Boquerón, 2,420 m, *Orozco, Tobón & Henao 1320* (COL), B (6 especímenes).

UTO 15 *Brunellia antioquensis*. Antioquia, Municipio La Ceja, Las Lomitas, 2,170 m, *Orozco, Tobon & Henao 1290* (COL) (4 especímenes).

UTO 16 *Brunellia antioquensis*. Antioquia, Municipio de Medellín, Piedras Blancas, 2,250 m, Orozco, Tobón & Henao 1280 (COL) (5 especímenes).

UTO 17 *Brunellia antioquensis*. Antioquia, Municipio de Río Negro, Sajonia, 2,290 m, *Orozco, Tobón & Henao 1286* (COL), C (6 especímenes).

para agrupar los datos de similitud de cada una de las matrices (Métodos 1, 2). El coeficiente de correlación cofenética fue calculado para cada uno de los fenogramas y es el resultado de comparar la matriz de similitud, derivada del fenograma, con la matriz de similitud de la que se originaron. El uso de este coeficiente es un estimado de la forma como cada técnica de agrupamiento traduce los valores de similitud.

El análisis de los componentes principales, Método 3, parte de una matriz de correlación entre caracteres, sin embargo, los resultados finales son las unidades taxonómicas operacionales representadas en el espacio y cuyas dimensiones corresponderían al resumen de los caracteres en vectores o componentes principales. El análisis permite tambien conocer el valor sistemático de cada uno de los caracteres. El árbol de la mínima distancia, Método 4, parte de una matriz de similitud de distancia entre UTO, y los resultados finales son las mínimas distancias fenéticas encontradas entre ellas; ver Sneath & Sokal (1973) y Crisci & Lopez Armengol (1983) para una mejor explicación de los procedimientos.

Los árboles de consenso (Adams, 1972) se usaron para comparar los agrupamientos obtenidos en los fenogramas; en otras palabras vienen a ser un resumen de la manera como operan las técnicas de agrupamiento para cada una de las matrices de similitud.

TABLA 2. Caracteres utilizados en los análisis taxonómicos numéricos, registrados para cada una de las 17 UTO. Codificación de los caracteres cuantitativos discontinuos y cualitativos.

Caracteres	Estados	Codificación
1. Longitud de la hoja (cm)	—	—
2. Longitud del pecíolo (cm)	—	—
3.* Longitud de los folíolos superiores (cm)	—	—
4. Ancho de los folíolos superiores	—	—
5.* Número de estípulas	2–3 estípulas	1
	4–7 estípulas	2
6. Número de lóbulos del cáliz	(3)4	1
	(4)5(6)	2
	5 y 6	3
7.* Diámetro del cáliz (mm)	—	—
8. Número de carpelos	(3)4(5)	1
	(4)5(6)	2
	5 y 6	3
9. Separación de los nervios (mm)	—	—
10.* Longitud del pedicelo (mm)	—	—
11. Grosor del pedicelo (mm)	—	—
12. Longitud del pedúnculo (cm)	—	—
13. Longitud de la inflorescencia (cm)	—	—
14. Longitud del folículo (mm)	—	—
15. Ancho del folículo (mm)	—	—
16. Indumento del folículo	Laxamente hirsuto	1
	Densamente hirsuto	2
17. Ancho de la semilla (mm)	—	—
18. Longitud de la semilla (mm)	—	—
19. Alto del endocarpo (mm)	—	—
20. Grosor de las ramas de primer grado de la inflorescencia (mm)	—	—
21. Grosor de las ramas de segundo grado de la inflorescencia (mm)	—	—
22. Grosor de las ramas de tercer grado de la inflorescencia (mm)	—	—
23. Forma de la semilla	Elíptica	1
	Cónica	2
24. Longitud de los folíolos inferiores (cm)	—	—
25. Ancho de los folíolos inferiores (cm)	—	—
26. Longitud de los filamentos (mm)	—	—
27. Longitud de las ramas del primer grado de la inflorescencia (cm)	—	—
28. Longitud de las ramas de segundo grado de la inflorescencia (cm)	—	—
29. Longitud de las ramas de tercer grado de la inflorescencia (mm)	—	—
30.* Pecíolulos	Presente	1
	Presente-Ausente	2
	Ausente	3
31. Superficie del folíolo en estado adulto	Liso	1
	Liso o rugoso	2
	Rugoso	3
32.* Margen del folíolo	Frecuentemente serrada, recta-diente delgado	1
	Frecuentemente serrada, cóncava-diente delgado	2
	Frecuentemente serrada, cóncava-diente grueso	3
	Frecuentemente crenado o serrado	4

* Caracteres diagnósticos en previos trabajos.
( ) escaso.

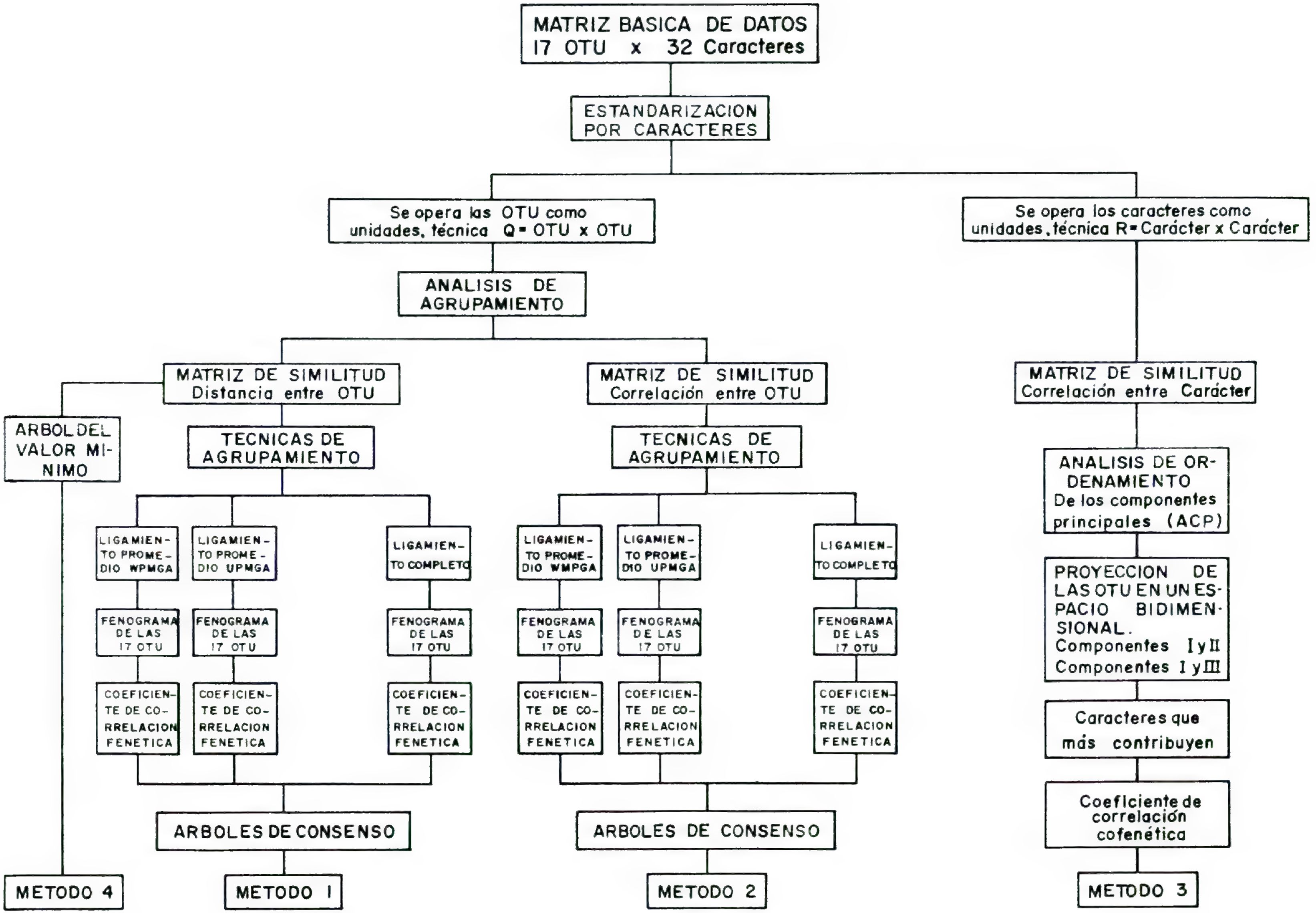


FIGURA 1. Estrategia metodológica de los análisis numéricos.

Muestras de granos de polen de las colecciones *Orozco et al. 1087, 1092, 1105, 1158, 1160, 1173, 1227, 1257, 1320, 1375,* y *Bernal 626* corresponden a diferentes muestras de las poblaciones (Tabla 1). Las muestras fueron enviadas al laboratorio Hugo de Vries, Amsterdam. Se utilizó la técnica Erdtman (1969) y el microscopio de barrido para obtener los micropreparados y fotografias. Directamente de las fotografias se tomaron datos del ancho del muro, ancho del lumen, longitud y ancho del grano, longitud del colpo, intercolpo y longitud y ancho del poro; estos datos fueron tambien complementados con los de las preparaciones que estaban en buen estado. Los datos del grosor de la exina se tomaron directamente de las fotografias.

Semillas de las poblaciones de las especies estudiadas, con excepción de las de Sibundoy, fueron colocadas en el germinador que consistía en una caja de petri con doble papel de filtro y agua destilada. El segundo papel de filtro fue previamente perforado en ocho huecos y en cada uno de ellos se colocaron las semillas. En estado de plántula fueron transplantadas en tierra y posteriormente llevadas al invernadero. Cuando las plantas estaban fuertes (6–7 meses de edad) se sometían a la poda de las puntas de la raíz. Este proceso se repetía cada 15 a 20 días para lograr raíces gruesas y figuras mitóticas claras en donde se pudieran contar los cromosomas. Las puntas se trataron con HCl 0.1 N y Carnoy 3:1.

Resultados y Discusión

consideraciones generales

Los resultados de los análisis de agrupamiento con los dos matrices de similitud muestran dos grandes grupos de UTO: *Brunellia comocladifolia* (UTO 1–6) y *B. sibundoya* (UTO 7–17). Cada grupo está conformado por las mismas UTO a excepción de los grupos obtenidos en el fenograma derivado de la matriz de correlación y la técnica del ligamiento completo (LC).

En todos los fenogramas se observa una mayor constancia de asociación (igual topología) para los subgrupos formados dentro del grupo de las UTO 1, 2, 3, 4, 5, y 6 (ver consensos Figs. 3–6) mientras que para el otro grupo, integrado por las restantes UTO la constancia de asociación entre las UTO es solamente observada en los fenogramas derivados de la matriz de correlación (Figs. 5, 6). La amplia variación dentro de este último conjunto sumado al efecto propio del coeficiente de distancia son las razones por las cuales cada uno de los subgrupos resultantes en los fenogramas de distancia varían en su totalidad en el contenido de las UTO (Figs. 3, 4). Aunque los coeficientes de correlación cofenética son ligeramente superiores a los obtenidos en los fenogramas derivados de la matriz de correlación, las verdaderas similitudes son enmascaradas. Sin embargo, se aprecia en los fenogramas de distancia la asociación constante entre las UTO 7 y 12, 8, 9, y 11 y 14, 16.

El fenograma WPMGA derivado de la matriz de correlación (Fig. 2) fue escogido como el que refleja con mas exactitud las similitudes morfológicas. Este agrupamiento de las UTO da un coeficiente de correlación cofenética (C.C.C.) de 0.7017. Los dos componentes principales del análisis de los componentes principales (ACP) (Tabla 3) representan el 58.13% de la variación entre las UTO (Fig. 7). El árbol de la mínima distancia (PRIM) está superpuesto sobre la figura del análisis de componentes principales; las mínimas distancias estan representados por los vínculos de unión entre las UTO y por los cuales se explica el porqué de los agrupamientos obtenidos en los fenogramas de distancia.

grupos taxonómicos

Los dos mayores grupos del análisis de agrupamiento corresponden a las especies *Brunellia comocladifolia* (UTO 1–6) y *B. sibundoya* (UTO 7–17); ver la Figura 2. También se observan los dos grupos por el componente I del análisis de los componentes principales (Fig. 7).

Existe una estrecha afinidad fenética entre las UTO 1, 2, 3 y 4, 5, 6, formando claramente dos subgrupos que corresponden, respectivamente, a las subespecies *Brunellia comocladifolia* subsp. *comocladifolia* y *B. comocladifolia* subsp. *cundinamarcensis*. En el análisis de los componentes principales por el componente II, también se reconocen las dos subespecies (Fig. 7). La posibilidad de diferenciar a la UTO 6 como representante de una tercera subespecie *boyacencis* se ve bastante disminuída por cuanto existe una alta similitud fenética entre las UTO 4, 5, 6, y de ahí la constante asociación entre ellas (Figs. 3–6). Por otra parte, la similitud también fue observada en la estructura de la exina entre las subespecies *cundinamarcensis* y *boyacensis* (Fig. 9). La cercanía geográfica y la ausencia de barreras geográficas (Fig. 14) explican la variación continua de las dos poblaciones y por ende el reconocimiento de un sólo taxon *B. comocladifolia* subsp. *cundinamarcensis*.

Una marcada superposición fenética se observa entre las UTO que representan los taxa *B. sibundoya* subsp. *sibundoya* (UTO 7, 8, 9) y *B. si-*

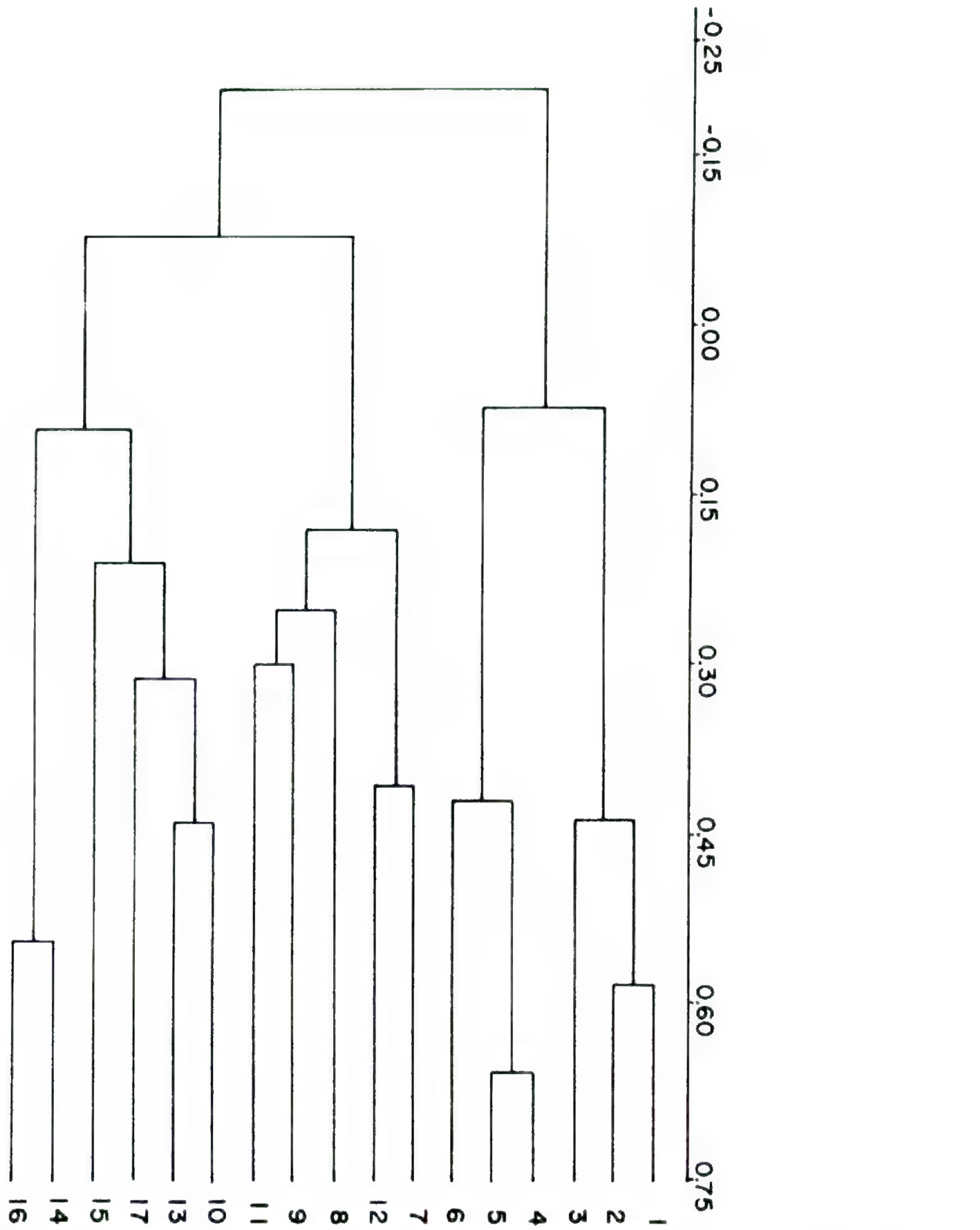


FIGURA 2. Fenograma de las 17 UTO basado en el coeficiente de correlación y la técnica de ligamiento ponderado WPMGA C.C.C. 0.7017.

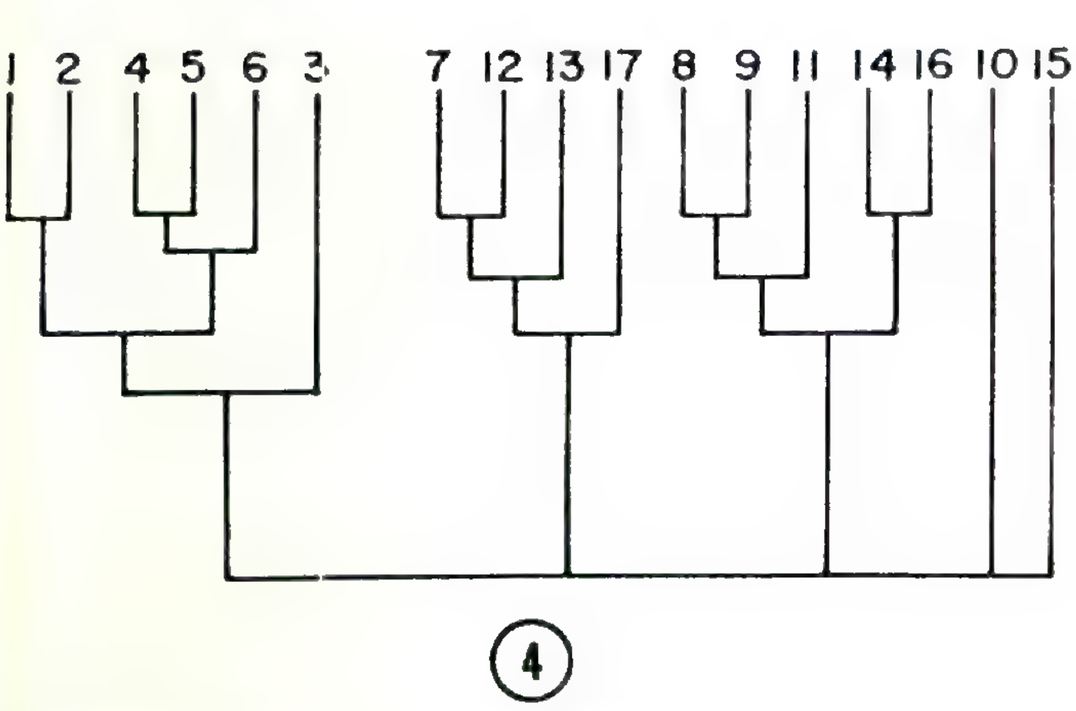
bundoya subsp. *sebastopola* (UTO 11, 12, 13). La superposición fenética es medida por la frecuente asociación en núcleos entre UTO que provienen de los diferentes grupos taxonómicos (Figs. 2–6). En el análisis de los componentes principales por el componente II, las UTO se muestran también relacionadas (Fig. 7). La estructura de la exina soporta estos resultados; no se encontró diferencia alguna en la estructura de los dos taxa (Fig. 10).

Los resultados muestran una segunda subespecie, *B. sibundoya* subsp. *antioquensis*, UTO 14, 15, 16, 17, y la UTO 10 (Figs. 2, 5–7). La UTO 13, en los análisis de correlación está relacionada con *B. sibundoya* subsp. *antioquensis* pero por el análisis de los componentes principales se encuentra mas asociada con *B. sibundoya* subsp. *sibundoya*.

En la Figura 7 (cuadrantes derecho, inferior y superior), las interconexiones debidas a las mínimas distancias fenéticas entre las UTO de los dos taxa infraespecíficos *B. sibundoya* son el resultado de una mayor relación fenética entre las subespecies que la encontrada en *B. comocladifolia*; en la misma figura cuadrante izquierdo inferior y superior se observa sólo una interconexión, entre las UTO 1 y 6, por tratarse de una unidad específica. Bajo diferente concepto taxonómico que el mostrado por los resultados de este trabajo, Cuatrecasas (1985) anota una estrecha afinidad entre *B. sibundoya* y *B. antioquensis*.

TABLA 3. Eigen-valores. Porcentaje de traza. Acumulación de porcentaje. Análisis de los componentes principales (ACP).

Componentes principales	Valores propios Eigen-Valores	% de Traza	Acumulación de %
Primer componente	14.185	44.33	44.33
Segundo componente	4.417	13.80	58.13
Tercer componente	3.527	10.44	68.57
Cuarto componente	2.267	6.71	75.28
Quinto componente	1.963	5.81	81.09
Sexto componente	1.518	4.49	85.58
Séptimo componente	1.334	3.95	89.53
Octavo componente	0.987	2.92	92.45
Noveno componente	0.696	2.06	94.51
Décimo componente	0.485	1.43	95.94
Décimo primer componente	0.398	0.84	96.78
Décimo segdo. componente	0.308	0.91	97.53
Décimo tercer componente	0.255	0.75	98.28
Décimo cuarto componente	0.180	0.53	98.81
Décimo quinto componente	0.153	0.45	99.26
Décimo sexto componente	0.118	0.34	99.60
Décimo séptimo componente	0.037	0.10	99.70
Décimo octavo componente	0.026	0.07	99.77
Décimo noveno componente	0.016	0.047	100.24



FIGURAS 3 y 4. Consenso entre las técnicas de agrupamiento basadas en el coeficiente de distancia.—3. Consenso Estricto.—4. Consenso de Mayoria.

FIGURAS 5 y 6. Consenso entre las técnicas de agrupamiento basadas en el coeficiente de correlación.—5. Consenso Estricto.—6. Consenso de Mayoria.

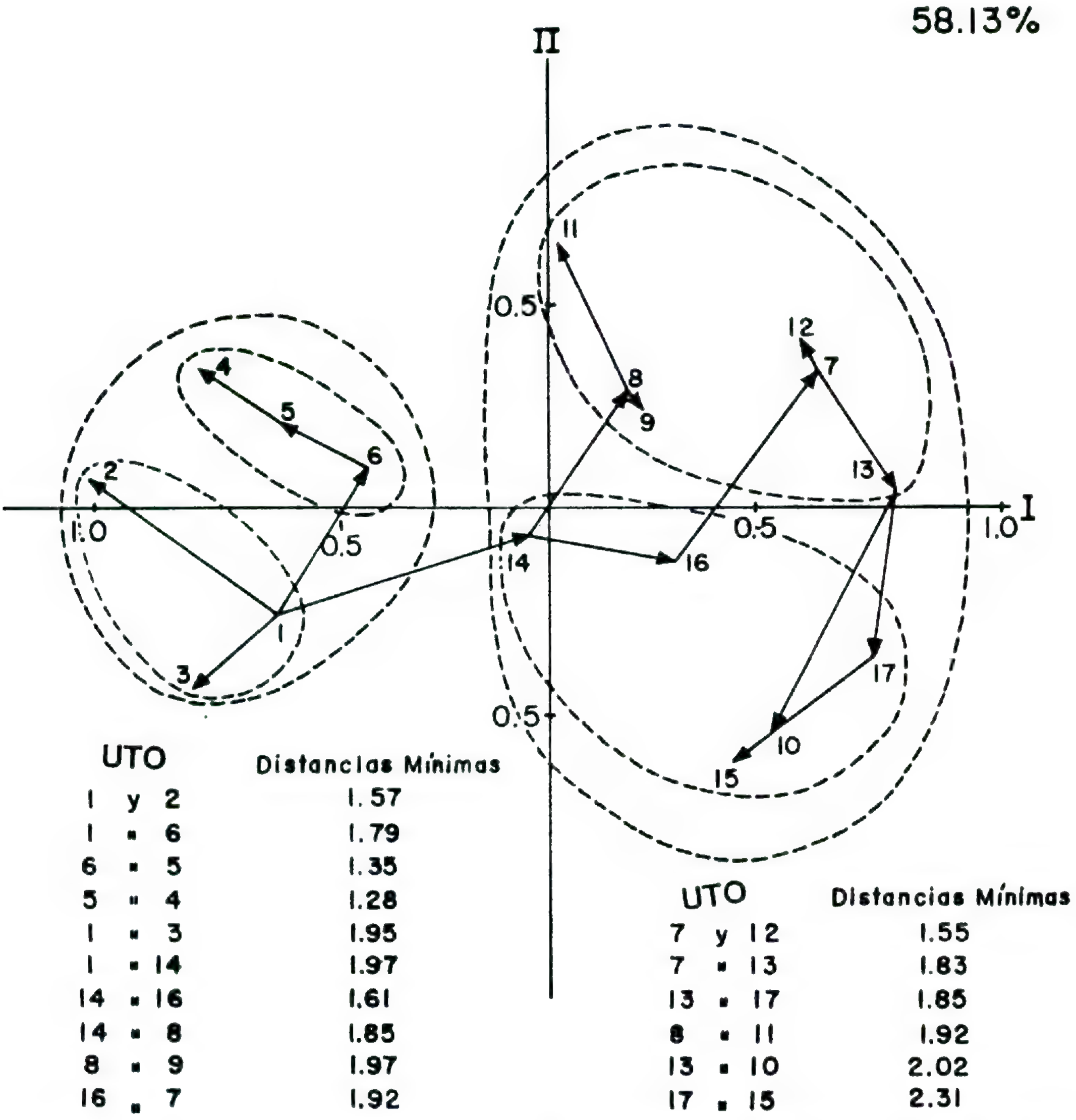


FIGURA 7. Análisis de los componentes principales (ACP) y el árbol del valor mínimo (PRIM). Las líneas entre las UTO representan las distancias mínimas entre ellas.

Los agrupamientos de distancia entre las UTO que integran las dos subespecies de *Brunellia sibundoya* (Figs. 3, 4) así como las interconexiones fenéticas son debidas a una amplia variación de los caracteres cuantitativos continuos. Asi, los extremos superiores e inferiores de estos caracteres son compartidos por las UTO de los dos diferentes grupos taxonómicos infraespecíficos, por ejemplo las mayores longitudes promedio de los folíolos superiores (15.16–19.04 cm) son exhibidas por las UTO 10, 15, 17 (*B. sibundoya* subsp. *antioquensis*) y las UTO 13, 12 (*B. sibundoya* subsp. *sibundoya*); las menores longitudes (9.69–12.30 cm) se encuentran en las UTO 14, 18 (*B. sibundoya* subsp. *antioquensis*) y las UTO 8, 7, 9, 11 (*B. sibundoya* subsp. *sibundoya*). En la Figura 7 estas UTO se encuentran unidas por las distancias fenéticas mínimas.

CARACTERES DISCRIMINANTES PARA EL RECONOCIMIENTO DE LOS GRUPOS TAXONÓMICOS

En el análisis de los componentes principales (Fig. 7), el componente I separa a los taxa *Brunellia comocladifolia* y *Brunellia sibundoya*. De los 32 caracteres morfológicos 3 de ellos (caracteres 23, 10, 5) en el componente I son importantes para diferenciar las especies (Tabla 4). La forma de la semilla en *B. comocladifolia* es elíptica, el indumento sobre los folículos es laxo y el número de estípulas no es superior a 3 (Figs. 16, 17). En

contraposición, la semilla en *B. sibundoya* es cónica, el indumento sobre los folículos es denso, y el número de estípulas es mayor de 3 (Figs. 18, 19).

Los caracteres cuantitativos continuos del grosor de las ramificaciones de la inflorescencia (caracteres 20, 21, 22) y el ancho de los folíolos superiores e inferiores (caracteres 4, 25), cuyos aportes al componente I son superiores a 0.8, no son muy útiles como diagnósticos por cuanto hay superposición de los límites superiores e inferiores. Sin embargo, en promedio el grosor de las ramificaciones y el ancho de los folíolos son menores en *B. comocladifolia* y pueden considerarse como tendencias. El ancho de los folíolos está relacionado con la forma lanceolada o angostamente oblonga observada con relativa frecuencia en *B. comocladifolia*. De manera similar en *B. sibundoya* los caracteres de grosor de las ramificaciones y ancho de los folíolos pueden considerarse como tendencia hacia mas gruesos y anchos, respectivamente. El ancho de los folíolos tiene que ver con las formas ovada, largamente ovada, ampliamente elíptica o ampliamente oblonga de los folíolos; estados observados con frecuencia en cada unidad taxonómica (UTO).

Dos caracteres (6, 8) en el componente II son útiles para la diferenciación infraespecífica (Tabla 4): *B. comocladifolia* subsp. *comocladifolia* exhibe 4 lóbulos del cáliz y 4 carpelos, en contraposición con la subespecie *cundinamarcensis* con 5 lóbulos del cáliz y 5 carpelos. En *B. sibundoya* subsp. *sibundoya* se encuentra con mayor frecuencia 5 lóbulos del cáliz y 5 carpelos, pero también se observó en algunas muestras hasta 6 lóbulos del cáliz y 6 carpelos. *Brunellia sibundoya* subsp. *antioquensis* se reconoce por la frecuencia de 4 lóbulos del cáliz y 4 carpelos y con menos frecuencia 5 lóbulos del cáliz y 5 carpelos.

Tres aspectos de los caracteres diagnósticos son importantes de mencionar en el momento: (1) los caracteres se encuentran correlacionados con las áreas o microáreas geográficas ocupadas por los taxa infraespecíficos (Fig. 15); (2) existe una alta correlación (análisis de agrupamiento de caracteres, técnica R) entre los caracteres diagnósticos tanto para la diferenciación específica como infraespecífica (Orozco, 1989); y (3) el escaso número de caracteres diagnósticos está relacionado con la estrecha afinidad morfológica entre las dos especies.

TABLA 4. Análisis de los componentes principales. Aporte de cada uno de los caracteres a los componentes principales.

Caracteres	Componentes		
	1	2	3
1	0.541	0.491	0.461
2	0.735	0.349	0.493
3	0.595	0.373	0.596
4	0.855	0.270	0.271
5	0.908	0.089	0.208
6	0.107	0.880	0.323
7	0.658	0.170	0.430
8	0.187	0.791	0.344
9	0.644	0.634	0.154
10	0.699	0.065	0.020
11	0.626	0.348	0.399
12	0.630	0.430	0.377
13	0.033	0.399	0.066
14	0.731	0.230	0.358
15	0.663	0.072	0.251
16	0.906	0.049	0.243
17	0.532	0.343	0.318
18	0.255	0.207	0.277
19	0.681	0.025	0.072
20	0.852	0.139	0.182
21	0.868	0.246	0.131
22	0.930	0.139	0.066
23	1.008	0.028	0.170
24	0.754	0.130	0.519
25	0.884	0.049	0.311
26	0.507	0.427	0.114
27	0.397	0.418	0.023
28	0.377	0.264	0.452
29	0.730	0.316	0.168
30	0.467	0.720	0.210
31	0.268	0.251	0.827
32	0.741	0.186	0.072

ESTRUCTURA DE LA EXINA

No se encontraron diferencias significantes en el tamaño del grano de polen, longitud del colpo, intercolpo, y longitud y ancho del poro. Las diferencias se observan a nivel de la estructura de la exina.

Brunellia comocladifolia exhibe una estructura reticulada con tendencia en la subespecie *comocladifolia* a lúmenes más amplios y muros continuos y aplanados (Fig. 8). La subespecie *cundinamarcensis* exhibe una exina reticulada irregular con lúmenes menos amplios y muros parcialmente fracturados y realzados (Fig. 9).

Se observa en *B. sibundoya* dos patrones diferentes de la estructura de la exina. Uno de ellos corresponde a la subespecie *sibundoya* con una estructura perforada rugulosa (Fig. 10); el otro patron a la subespecie *antioquensis* con una estructura reticulada irregular (Fig. 11) y muy similar a la observada en *B. comocladifolia* subsp. *cundinamarcensis*.

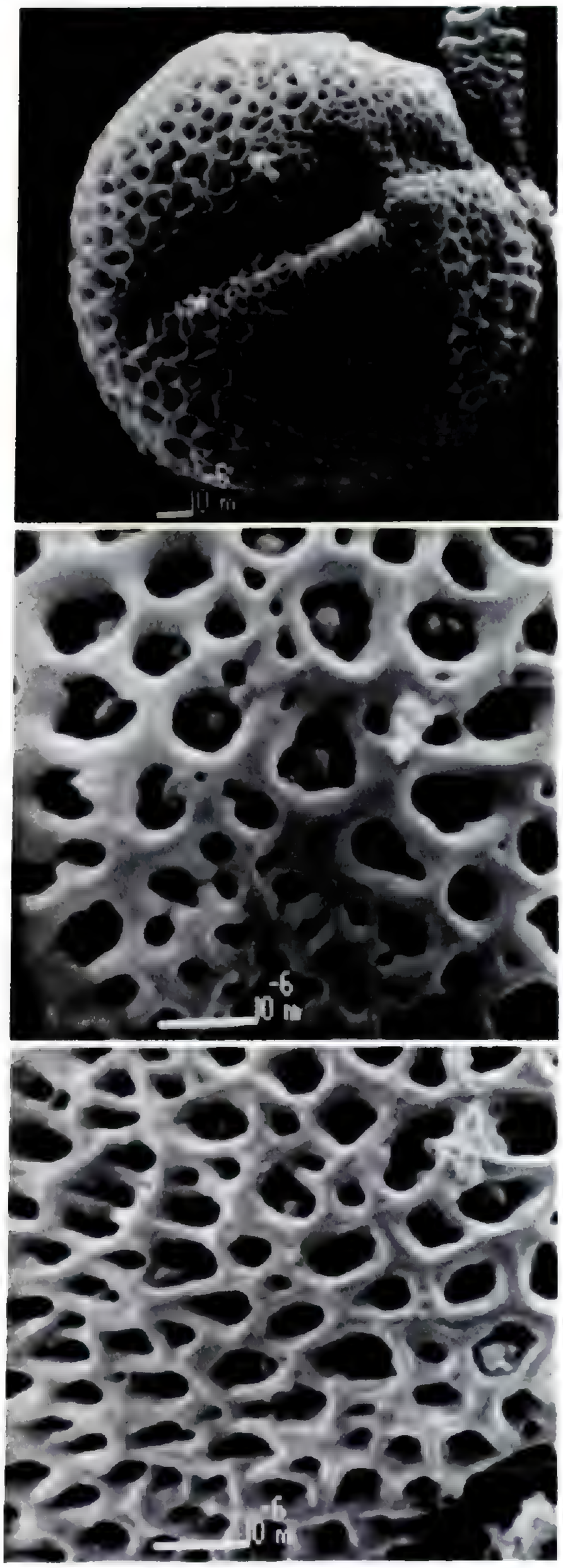


FIGURA 8. Forma y estructural del grano del polen de *Brunellia comocladifolia* Humb. & Bonpl. subsp. *comocladifolia*. a y b, *Orozco et al. 1227*; c, *Orozco et al. 1158*.

Cuatrecasas (1985) se refiere también a las variaciones infraespecíficas de la estructura de la exina encontradas por Marticorena (1970), bajo el microscopio de luz, en otras subespecies neotropicales de *B. comocladifolia*. Muller (1979) y Nowicke & Skvarla (1979), quienes han observado las variaciones estructurales de la exina a nivel infraespecífico, atribuyen dicha variación a un amplio componente de adaptación del grano de polen, especialmente el de la superficie del tectum. Posiblemente también sea el caso de la variación encontrada en *Brunellia*.

CROMOSOMAS

El número cromosómico $2n = 28$ es reportado para *Brunellia comocladifolia* subsp. *cundinamarcensis* y *B. sibundoya* subsp. *sibundoya*. Para las dos otras subespecies no se reporta el número cromosómico debido a que las plántulas no tuvieron éxito. Los resultados presentados fueron obtenidos sin pretratamiento alguno (Figs. 12, 13). Las diferencias en el tamaño de los cromosomas se deben a diferentes estadios metafásicos.

Los datos del número de cromosomas coinciden con los reportados por Ehrendorfer et al. (1984) para *Brunellia mexicana* Standl. y *B. comocladifolia* subsp. *funckiana* (Tul.). Ehrendorfer et al. (1984) señalan la dificultad en obtener un cariotipo claro, dificultad también observada en este estudio por la escasa precisión en la morfología de los cromosomas.

DISTRIBUCIÓN GEOGRÁFICA

Las dos subespecies de *Brunellia comocladifolia* se encuentran en las selvas subandinas entre 1,000–1,800 m, mientras que *B. sibundoya* se registra a alturas mayores entre 2,000–2,900 m, ocupando las selvas andinas y subandinas.

Brunellia comocladifolia subsp. *comocladifolia* no sólo se distribuye en el sur de Colombia y Ecuador (Cuatrecasas, 1985) sino que se extiende hacia el norte por la cordillera occidental hasta Antioquia. *Brunellia comocladifolia* subsp. *cundinamarcensis* se distribuye sobre la cordillera oriental y se reporta para el norte en el Huila, Cundinamarca y en Boyacá; posiblemente se extiende más hacia el sur y más hacia el norte en los departamentos de Santander. Los datos disponibles para el estudio permiten visualizar la separación geográfica entre las dos subespecies por la cordillera central (Fig. 14). Se infiere que la diferenciación infraespecífica pudo haber ocurrido en el sur de Colombia en los sitios geográficos que corresponden a la ramificación de los Andes colombianos.

Brunellia sibundoya subsp. *sibundoya* tiene una más amplia distribución (Fig. 14). Originalmente la subespecie fue reportada en el Nudo de los Pastos (Putumayo), en la cordillera central flanco oriental, e interconexiones con la cordillera occidental, Cauca (Cuatrecasas, 1970), sitios donde se registraron las menores alturas (2,000–2,300 m). Nuevas colecciones en el Tolima señalan el ascenso de la subespecie a lo largo de la vertiente

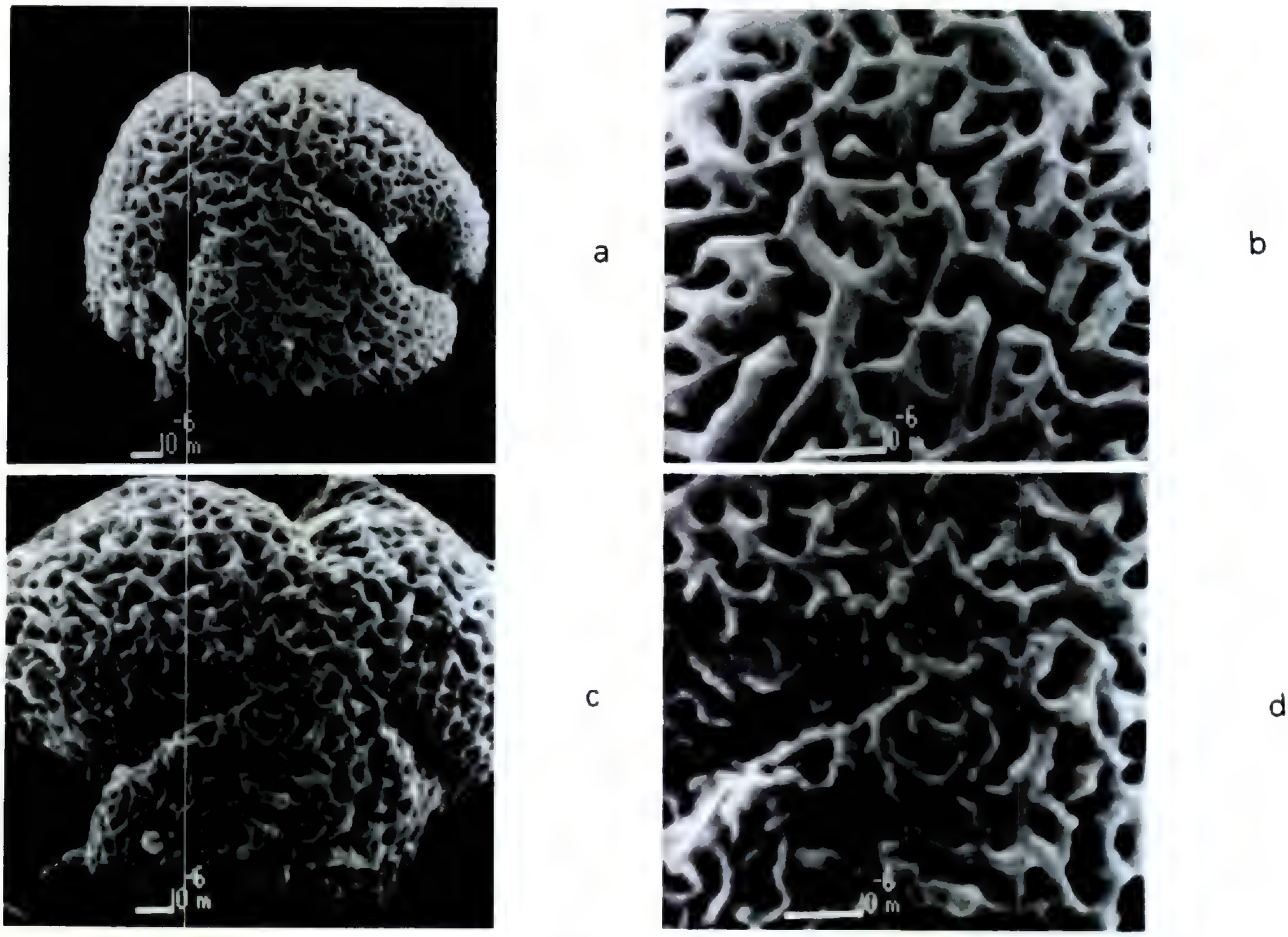


FIGURA 9. Forma y estructura del grano del polen de *Brunellia comocladifolia* Humb. & Bonpl. subsp. *cundinamarcensis*. Cuatrec. a y b, *Orozco et al. 1105*; c y d, *Orozco et al. 1267*, colección muestreada como *Brunellia comocladifolia* subsp. *boyacensis*.

oriental de la cordillera central. Los resultados del actual estudio indican también la presencia del taxon en la cordillera oriental (Cundinamarca) y por los datos disponibles se infiere que la presencia de la subespecie en la cordillera oriental se deba más bien al ascenso por la misma desde el Nudo de los Pastos. Esta inferencia se apoya en el registro del taxon para el sur del Huila en los límites con el departamento del Cauca, cercano al lugar del nacimiento del ramal de la cordillera oriental y la separación entre la cordillera central y oriental (Río Magdalena, Fig. 14).

En contraposición con los restantes subespecies los datos disponibles permiten reconocer el taxon *B. sibundoya* subsp. *antioquensis* en una área geográfica mas estrecha y con una amplia distribución hacia el norte de las cordilleras central y occidental. El taxon en previos trabajos fue registrado hacia el norte en la cordillera central (Antioquia), sitios en donde la cordillera no tiene sus más altas elevaciones; nuevas colecciones indican su distribución en la cordillera occidental (Caldas y Antioquia) y más hacia el sur en la cordillera central-vertiente occidental (Valle del Cauca y Caldas). La presencia del taxon en la cordillera occidental y en la cordillera central puede estar relacionada con la diferenciación infraespecífica en el sur de Colombia o, por la subespeciación mas hacia el norte, en la cordillera central. Esta última pudo haber sido favorecida por la disimetría climática en los dos flancos de la cordillera a causa de los efectos de la glaciación (Salomons, 1986). Bajo esta consideración, debe de haber existido una amplia dispersión por su ocurrencia en la cordillera occidental. Las subespecies *antioquensis* y *sibundoya* se encuentran en los sitios más elevados de la cordillera central y donde las vertientes son más acentuadas (Fig. 14).

Al parecer la diferenciación específica está relacionada con el gradiente altitudinal, mientras que la infraespecífica lo está con la cantidad de humedad. Estos dos factores climáticos (Sarmiento, 1986) vienen a ser los factores de mayor importancia ecológica variando a través y a lo largo de las cordilleras andinas. La humedad, que caracteriza a la cordillera occidental y vertiente occidental de la cordillera central, aunque debida a diferentes causas tiene que ver con la reducción

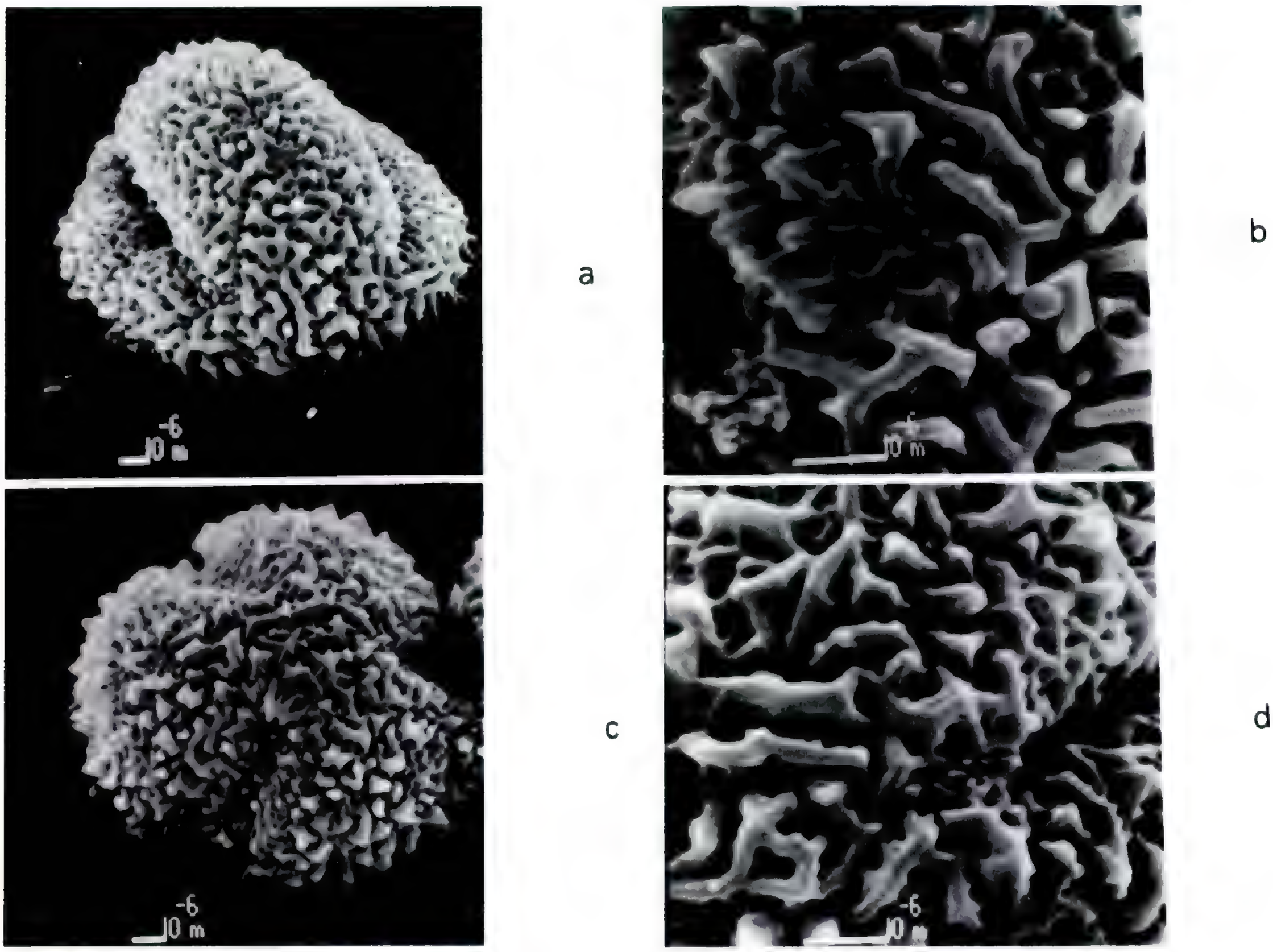


FIGURA 10. Forma y estructura del grano de polen de *Brunellia sibundoya* Cuatrec. subsp. *sibundoya*. a y b, *Orozco et al. 1173*; c y d, *Orozco et al. 1087*, colección muestreada como *Brunellia sibundoya* subsp. *sebastopola*.

del número de partes florales: *B. comocladifolia* subsp. *comocladifolia* y *B. sibundoya* subsp. *antioquensis* tienen solamente cuatro lóbulos del cáliz y cuatro carpelos.

Los datos de distribución permiten establecer cuatro áreas o microáreas geográficas libres de superposición y correlacionadas con cuatro diferentes combinaciones de caracteres morfológicos y de estructura de la exina (Fig. 15).

TRATAMIENTO SISTEMÁTICO

CLAVE PARA LAS ESPECIES Y SUBESPECIES DE *BRUNELLIA* ESTUDIADAS

1a. Estípulas 2–3; indumento del folículo laxamente hirsuto; semilla elíptica; 1,000–1,800 m.
  2a. Lóbulos del cáliz y carpelos 4; cordillera occidental e interconexiones al sur de las cordilleras central y occidental. ..... 1a. *B. comocladifolia* subsp. *comocladifolia*
  2b. Lóbulos del cáliz y carpelos 5; cordillera oriental ..... 1b. *B. comocladifolia* subsp. *cundinamarcensis*
1b. Estípulas 4–7; indumento del folículo densamente hirsuto; semilla cónica; 2,000–2,800 m.
  3a. Lóbulos del cáliz y carpelos 5–6; en el sur del Macizo colombiano e interconexiones de las cordilleras occidental y central y vertiente oriental de la cordillera central ..... 2a. *B. sibundoya* subsp. *sibundoya*
  3b. Lóbulos del cáliz y carpelos 4(5); hacia el norte en la cordillera occidental y vertiente occidental de la central ..... 2b. *B. sibundoya* subsp. *antioquensis*

1. Brunellia comocladifolia Humb. & Bonpl. Pl. Aequinoct. 1: 211–213, pl. 59. 1808; HBK Nov. Gen. Sp. 7: 46. 1825; Cuatrec. Fl. Neotropica, 2: 63–68. 1970; Supplement 43–46. 1985.

Arbol 5–12 m. Estípulas 2–3. Hojas compuestas opuestas, 12.4–73.2 cm de largo, imparipinadas 1–7 yugos, 3.15(–18) folíolos; pecíolo 3.3–14.0 cm de largo. Folíolos peciolulados o sésiles, los superiores 3.6–16.0 cm de largo, (1.4–)2.0–7.4 cm de ancho, oblongo-elípticos, elípticos, lanceolados; base del folíolo obtuso o cuneado. Folíolos inferiores ovados (1.7–)2.5–10.5 cm de largo, (1.0–)1.6–5.0 cm de ancho; márgen de los folíolos crenado-serrada, serrada o márgen cóncavo-serrada; nervios secundarios prominentes por el envés; (6–)9–18(–20) pares, distantes entre si (1.5–)3.0–

18 mm; indumento sobre los nervios de pelos largos, flexibles. Superficie de los folíolos lisa y menos frecuente rugosa. Inflorescencia tirsoide, 6.3–30.0 cm de largo; ramificaciones delgadas, en cimas dicasiales, isotónicas, ramas de primer grado 1.2–30 mm de grueso, de segundo grado 1.0–2.0(–3.0) mm de grueso, de tercer grado de 0.8–1.5(2.0) mm de grueso. Pedúnculo 1.5–12.5 cm de largo. Flores hermafroditas o unisexuales, pediceladas en fruto, en flores femeninas y con menos frecuencia en flores masculinas; pedicelos 2.0–3.5 mm de largo, 0.2–0.5(–1.0) mm de grueso. Cáliz pentámero o tetrámero, diámetro del cáliz en fruto (3.5–)4.0–5.5(–6.0) mm. Estambres 10, filamentos (1.5–)2.0–3.0 mm de largo. Carpelos 4 o 5. Folículos 4 o 5, con indumento laxamente hirsuto, ovados, 2.2–3.0 mm de largo, 2.0–3.0 mm de ancho. Endocarpo seco en forma de U, 2.0–2.7(–2.9) mm de alto. Semilla 1 desarrollada por folículo, elíptica, 1.8–2.2 mm de largo, 1.5–2.0 mm de ancho.

1a. Brunellia comocladifolia Humb. & Bonpl. subsp. **comocladifolia** Fl. Neotropica 2: 66–67. 1970; Supplement 43–45. 1985. TIPO: Colombia. Cauca: Popayan, 1906, *Humboldt & Bonpland s.n.* (holótipo, P; isótipo, P n.v.). Figura 16.

Arbol 5–12 m. Folíolos peciolulados 1.0–4.0 mm de largo; folíolos inferiores de una misma rama de menor tamaño comparados con los superiores; margen de los folíolos en su máximo desarrollo tendiente a ser cóncava y serrada. Cáliz tetrámero. Carpelos 4. Folículos 4 con muy escasa frecuencia en menor número. Granos de polen con exina regularmente reticulada.

Distribución *Brunellia comocladifolia* subsp. *comocladifolia* tiene una amplia distribución desde el sur (Ecuador), y a lo largo de de la cordillera occidental en Colombia, hasta el departamento de Antioquia. También al sur en la intersección entre la cordillera central y la occidental.

Ejemplares representativos. COLOMBIA. ANTIOQUIA: Municipio La Concordia, vía Urrao, 1,750 m, 3 dic. 1984 (fr), *Orozco, Tobón & Henao 1341* (COL). RISARALDA: Municipio de Pueblo rico, carretera al cerro Montezuma, 1,350 m, 5 mar. 1986 (fl ♂), *Bernal, Galeano, Tobón & Henao 1101* (COL). VALLE DEL CAUCA: cordillera occidental, hoya del río Calima, El Cairo entre Darién y Mediacanoa, 1,650–1,750 m, 7 ene. 1943 (fr), *Cuatrecasas 13867* (COL); Municipio de Dagua, Pichindé, 1,650 m, 22 sep. 1983 (fr), *Orozco, Vidal & Lozano 1156* (COL).

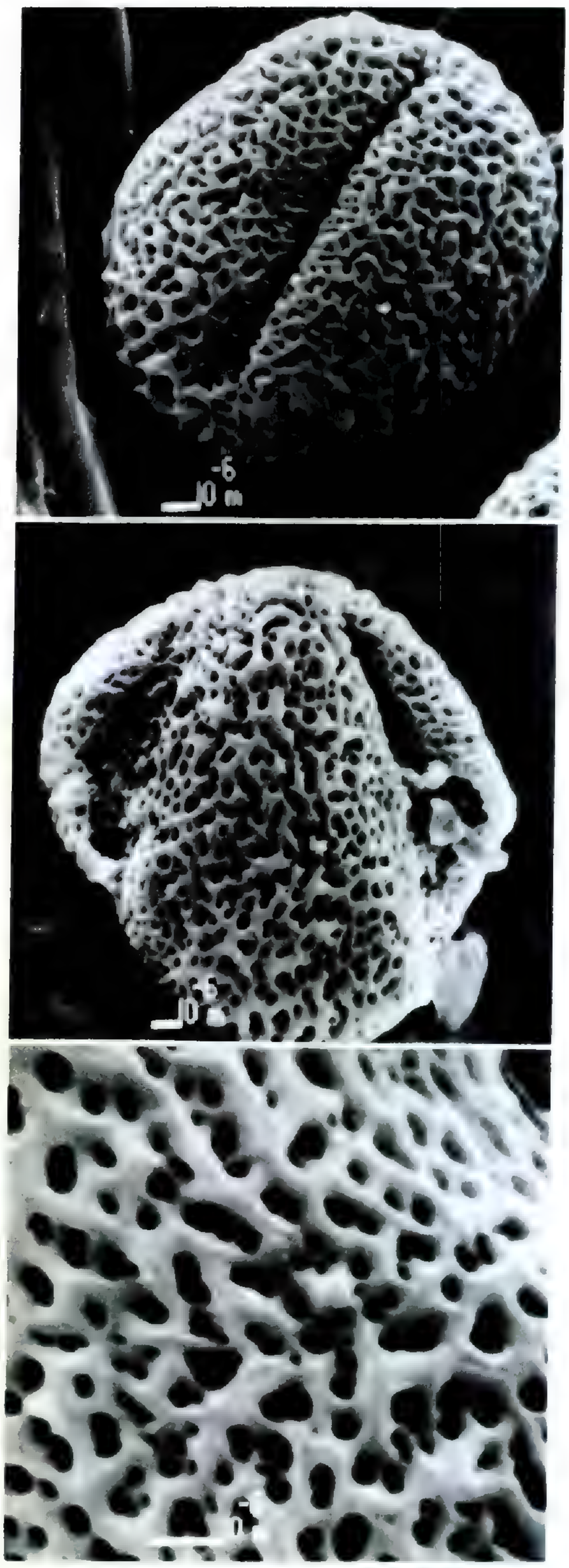


FIGURA 11. Forma y estructura del grano de polen de *Brunellia sibundoya* subsp. *antioquensis* Cuatrec. a, *Orozco et al. 1320*; b y c, *Orozco et al. 259*, colecciones muestreadas como *Brunellia antioquensis*.

1b. Brunellia comocladifolia Humb. & Bonpl. subsp. **cundinamarcensis** Cuatrec. Fl. Neotropica 2: 68–69. 1970; Supplement 45. 1985. TIPO. Colombia. Cundinamarca: Susumuco, 1,000 m, dic. 1855 (fl), *Triana 3720* (holótipo, W; isótipos, BM, G, US, W). Figura 17.

Brunellia comocladifolia Humb. & Bonpl. subsp. *boyacensis* Cuatrec. Fl. Neotropica 2: 67–68. 1970. TIPO: Colombia. Boyacá: Monte del Chapón, 1,230

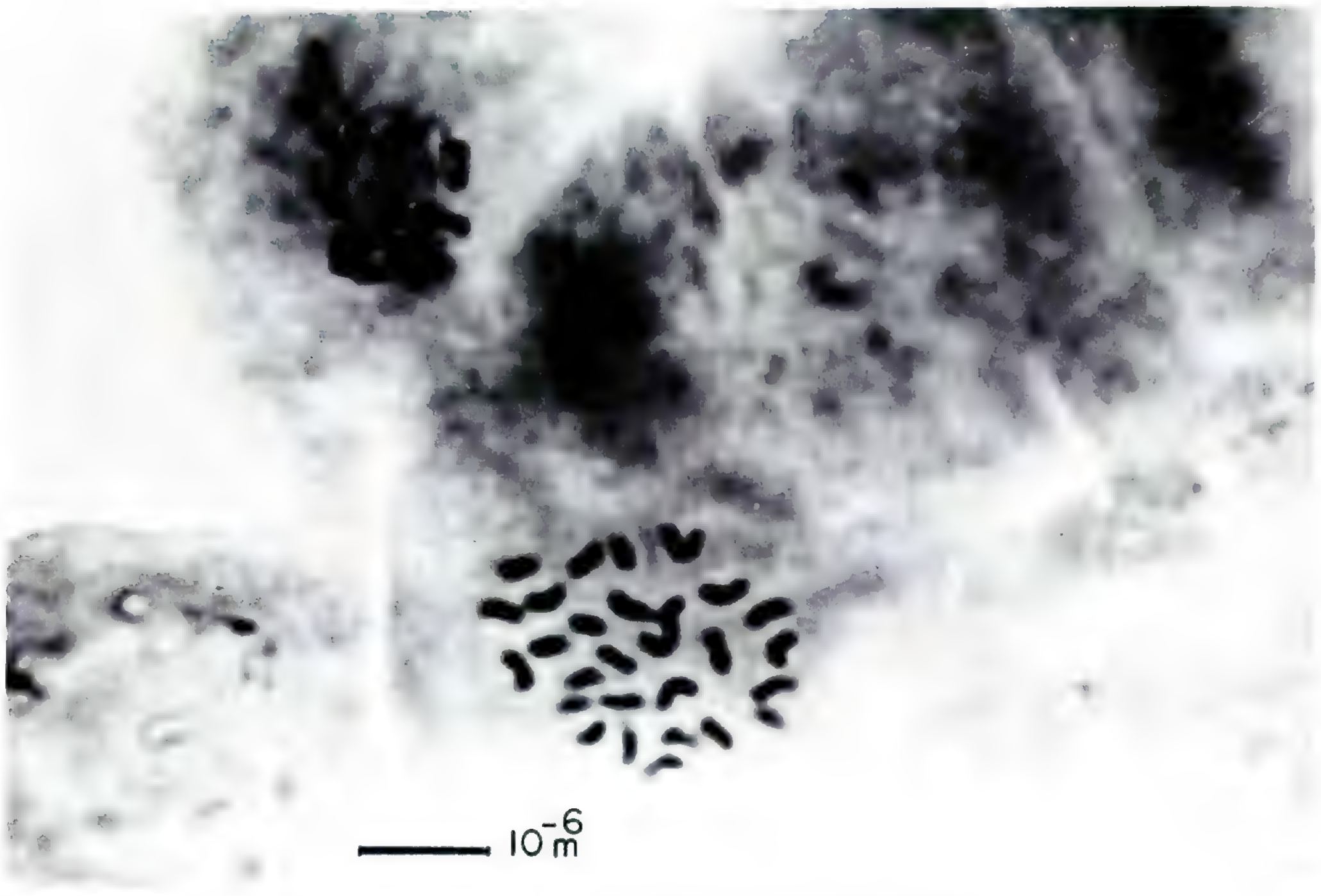


FIGURA 12. Cromosomas metafásicos de *Brunellia sibundoya* subsp. *sibundoya*.

m, 21 jul. 1932 (fr), *Lawrence 347* (holótipo, NY; isótipos, BM, F, G, GH, MO, S, U, US).

Arbol 6–10 m. Folíolos sésiles o muy cortamente peciolulados, 0–1.5 mm de largo, base obtusa o cuneada, margen serrada o crenado-serrada. Lóbulos del cáliz 5. Carpelos 5. Granos de polen con exina irregularmente reticulada.

Distribución. Cordillera oriental en los departamentos de Cundinamarca, Boyacá y en Huila. Existe en COL un especimen de la colección *Little 7253* procedente de Huila que parece más bien corresponder por los datos de altura, 2,000–2,030 m, a *B. sibundoya* subsp. *sibundoya*.

Ejemplares representativos. COLOMBIA. BOYACA: Municipio La Victoria, Alto del Chapón, 29 jul. 1984 (fr), *Orozco, Sanabria & Sanchez 1256* (COL); hacia la quebrada de la Colichona, vereda San Martín, 1,500 m, 29 jul. 1984 (fr), *Orozco, Sanabria & Sanchez 1265* (COL); hacia Quípama, 1,350 m, 30 jul. 1984 (fl, ♂), *Orozco,*

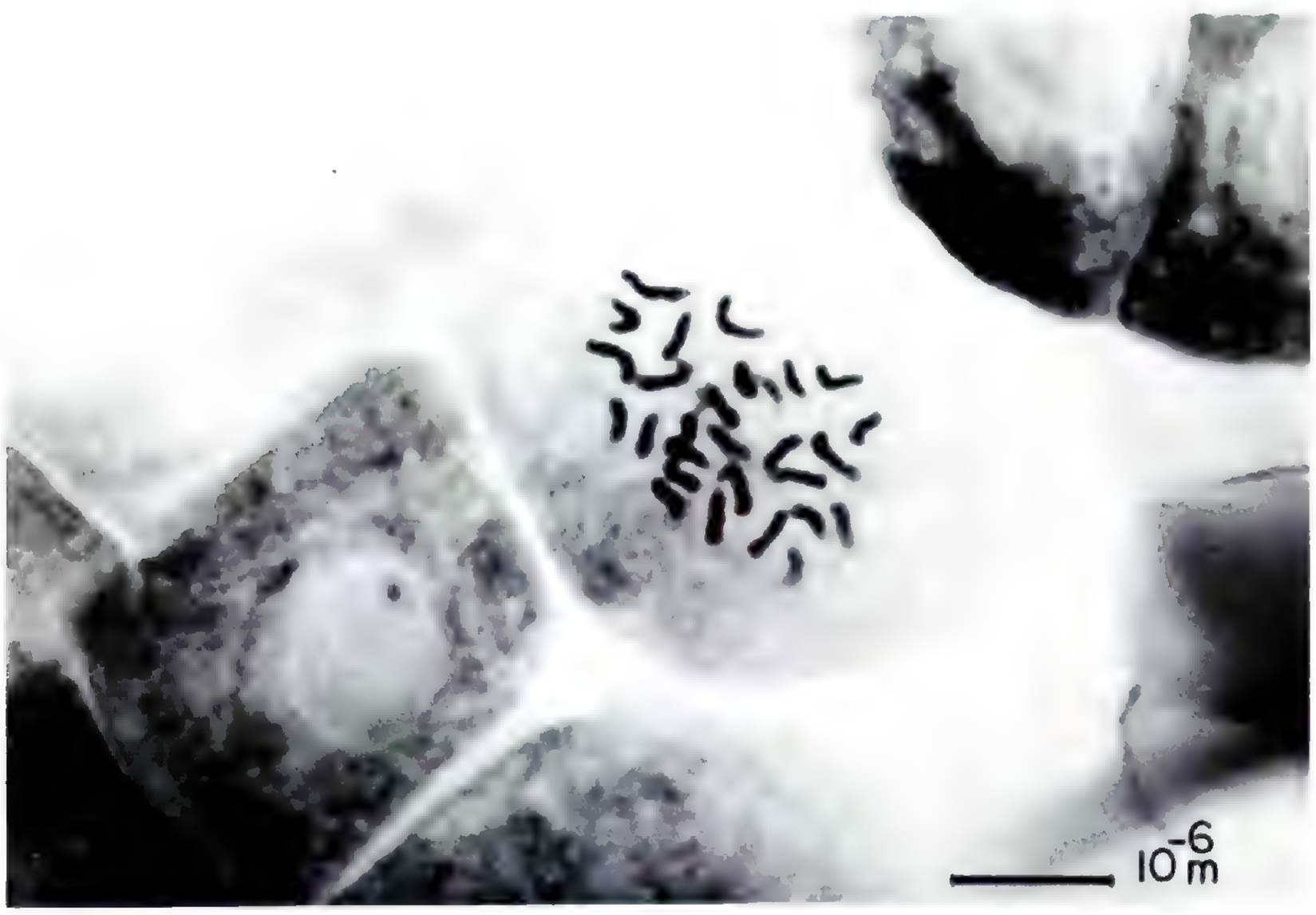


FIGURA 13. Cromosomas premetafásicos de *Brunellia comocladifolia* subsp. *cundinamarcensis*.

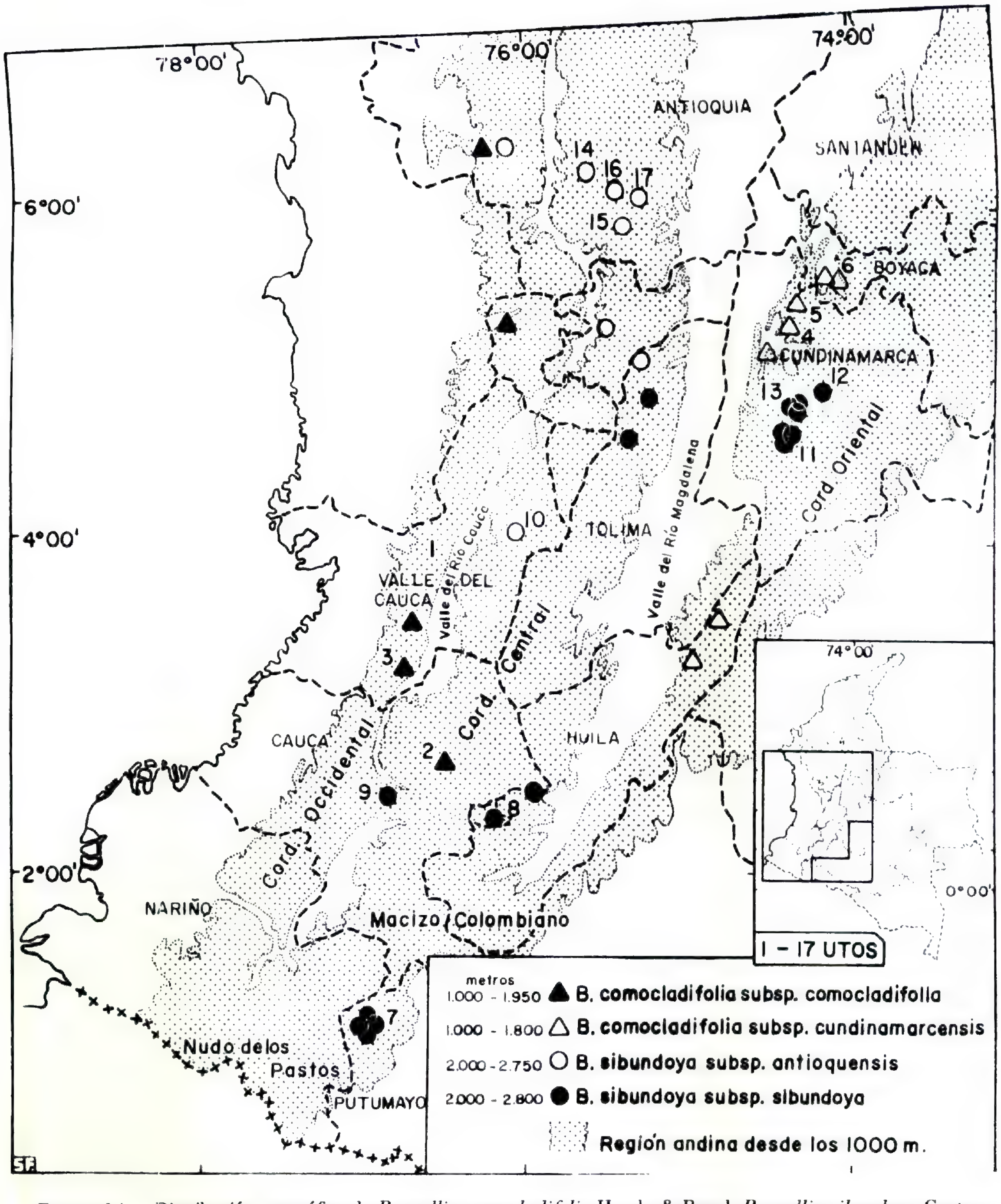


FIGURA 14. Distribución geográfica de *Brunellia comocladifolia* Humb. & Bonpl. *Brunellia sibundoya* Cuatrec. Los números se refieren a las UTO.

Sanabria & Sanchez 1267 (COL). CUNDINAMARCA: Municipio de la Palma, 1,730 m, 30 mayo 1983, *Orozco, Lozano & Franco 1102* (COL); Sasaima, 1,600 m, 3–5 ene. 1973 (fl, ♂), *García Barriga 20379* (COL). HUILA: Río Venadito, 25 km SE de la Bodega, 1,780 m, 2 dic. 1944 (fr), *Little 9024* (COL).

Nombre vulgar. Tambor, en Cundinamarca y Boyacá.

2. Brunellia sibundoya Cuatrec. Revista Acad. Colomb. Ci. Exact. 5: 35. 1942; Cuatrec. Fl. Neotropica 2: 78–79. 1970; Supplement 46–48. 1985.

Arbol 6.0–20 m. Estípulas 4–7. Hojas compuestas opuestas, (9.0–)20–74.3(–83.8) cm de

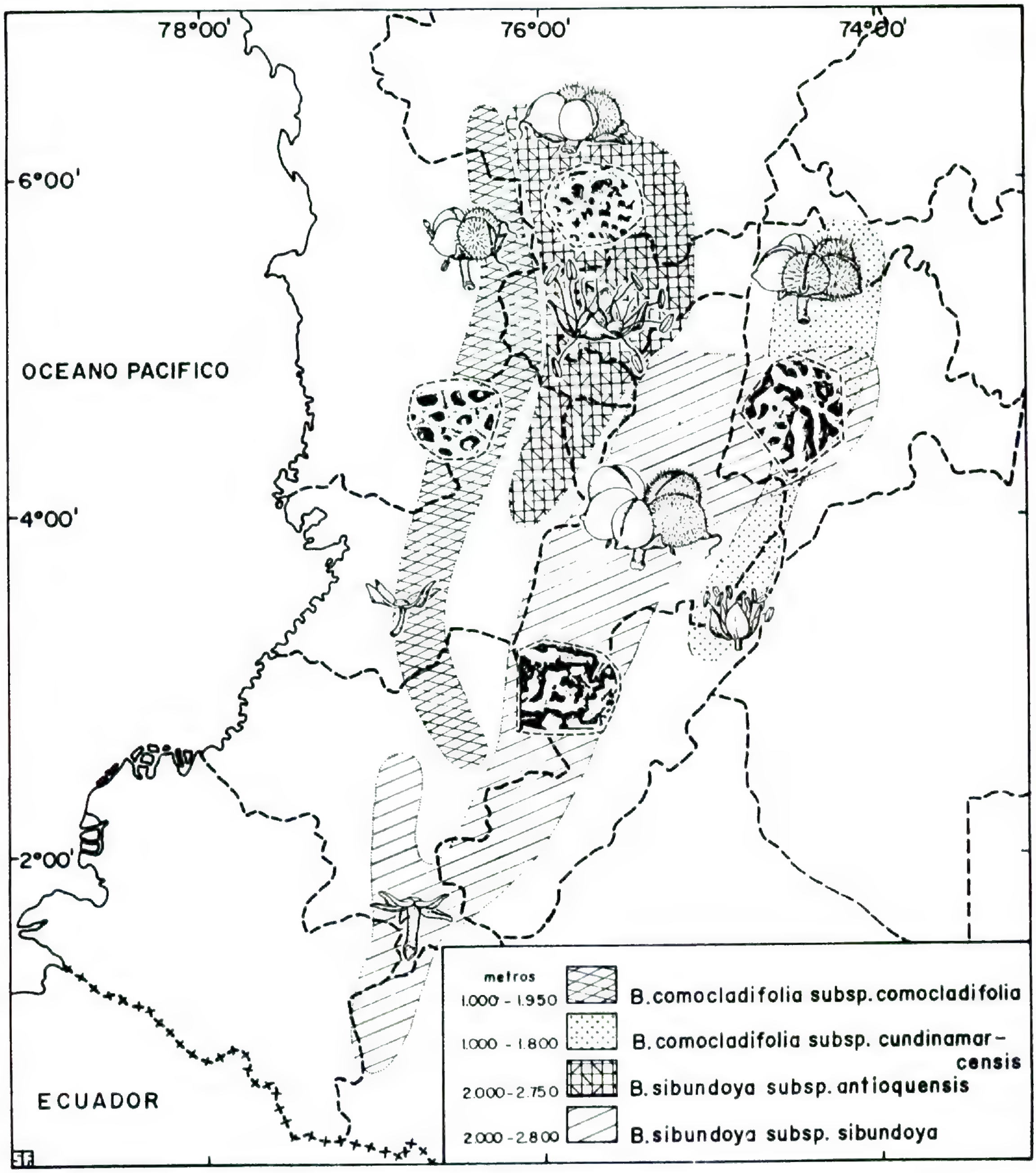


FIGURA 15. Distribución geográfica y caracteres diagnósticos de las especies de *Brunellia* estudiadas.

largo, imparipinadas, 1–7 yugos, 3–15 folíolos. Pecíolo 3.0–19.5 cm de largo. Folíolos sésiles o peciolulados, los superiores 6.0–28.0 cm de largo, (2.5–)3.3–10.6 cm de ancho, ovados, ovado-oblongos, elípticos u oblongo-elípticos; base obtusa o cuneada; margen de los folíolos crenado-serrada o cóncavo-serrada; nervios secundarios prominentes por el envés, (6–)9–22 pares, se apartan entre sí (2.0)3.0–21.0 mm. Folíolos inferiores ovados; 4.3–17.0 cm de largo, 1.8–9.9 cm de ancho. Superficie de los folíolos lisa o rugosa. Inflorescencia en tirso o en dicasio, 6.5–31.0 cm de largo; ramificaciones gruesas, en dicasios de una casi perfecta isotonía, ramas de primer grado, (1.5–)(2.0–4.2) (–5.5) mm de grueso, de segundo grado (1.0–)2.0–3.5 mm de grueso, de tercer grado 1.2–3.0(–4.0) mm de grueso. Pedúnculo 1.5–18.0 cm long. Flores hermafroditas o unisexuales, pediceladas en fruto o en flores femeninas, sésiles en flores masculinas, pedicelos 1.0–2.0(–2.5) mm de largo, (0.8–)(1.0–1.5)(–2.0) mm de grueso. Cáliz pentámero o tetrámero (hexámero), diámetro en

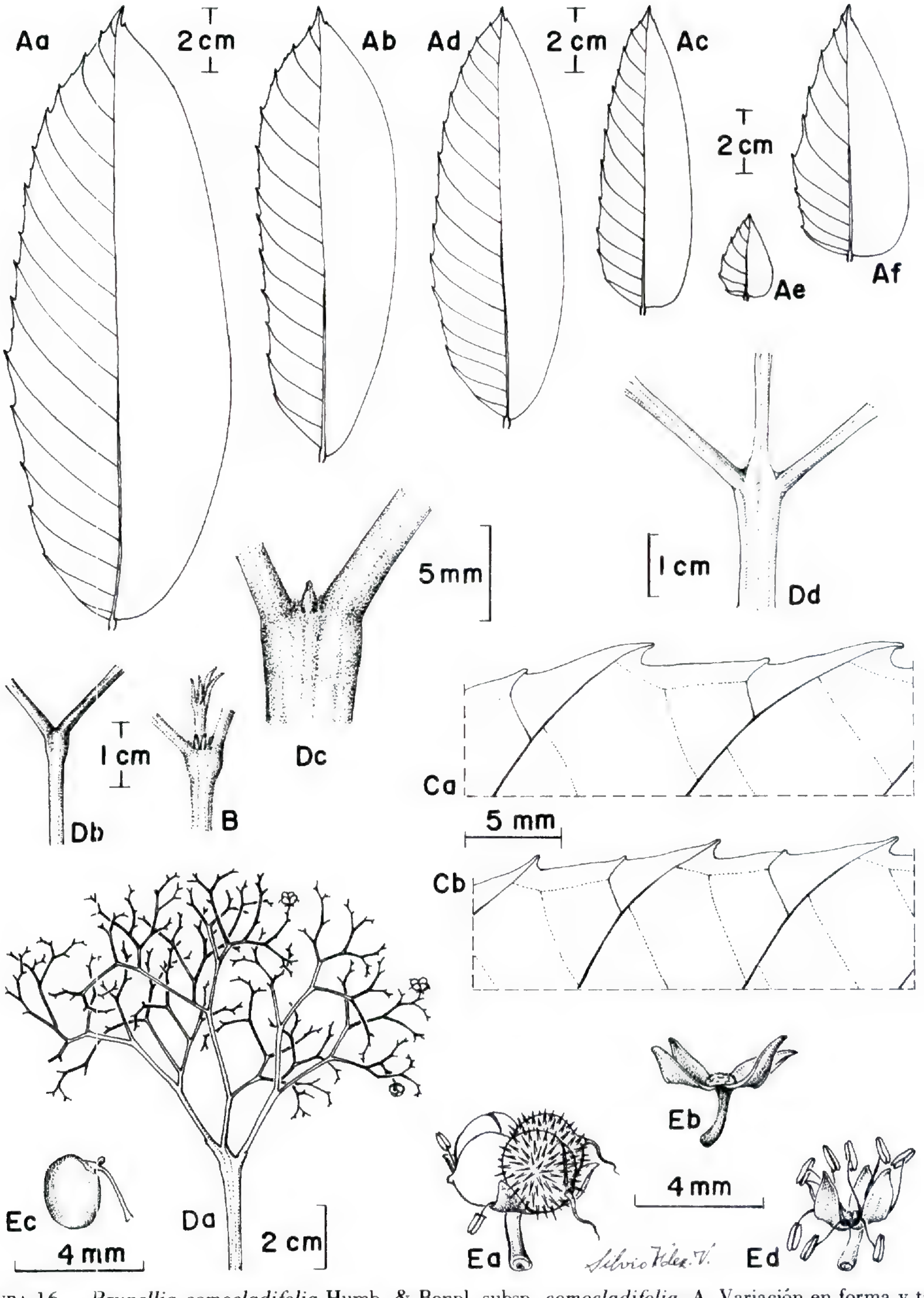


FIGURA 16. *Brunellia comocladifolia* Humb. & Bonpl. subsp. *comocladifolia*. A. Variación en forma y tamaño de los folíolos.—Aa–Ad. Folíolos superiores.—Ae, Af. Folíolos inferiores.—B. Detalle de las estípulas y yema.—C. Margen del folíolo.—Da. Inflorescencia completa.—Db–Dd. Ramificación de la inflorescencia.—E. Partes de la flor y fruto.—Ea. Folículos y estambres.—Eb. Número de lóbulos del cáliz.—Ec. Semilla.—Ed. Flor masculina. A (a, d, f), B, C (b), D (a–d), y E (a–c) *Orozco et al. 1156*; A (b), *Orozco et al. 1160*; A (c), *Duque-Jaramillo 3893*; A (e) y C (a), *Cuatrecasas 13857*; E (d), *Orozco et al. 1158*.

fruto (5.0–)5.5–7.0(–7.5) mm. Estambres 10, filamentos (2.0–)2.8–5.0 mm de largo. Folículos 4 o 5(6), con indumento denso e hirsuto, ovados, 2.8–4.0(–4.2) mm de long, (2.2–)3.0–4.0 mm de ancho. Endocarpo seco en forma de U, (2.0–)2.5–3.0(4.0) mm de alto. Semilla 1 desarrollada por folículo, cónica, (1.2–)2.0–2.5(–3.0) mm de largo, (1.2–)1.8–2.0(–2.2) mm de ancho.

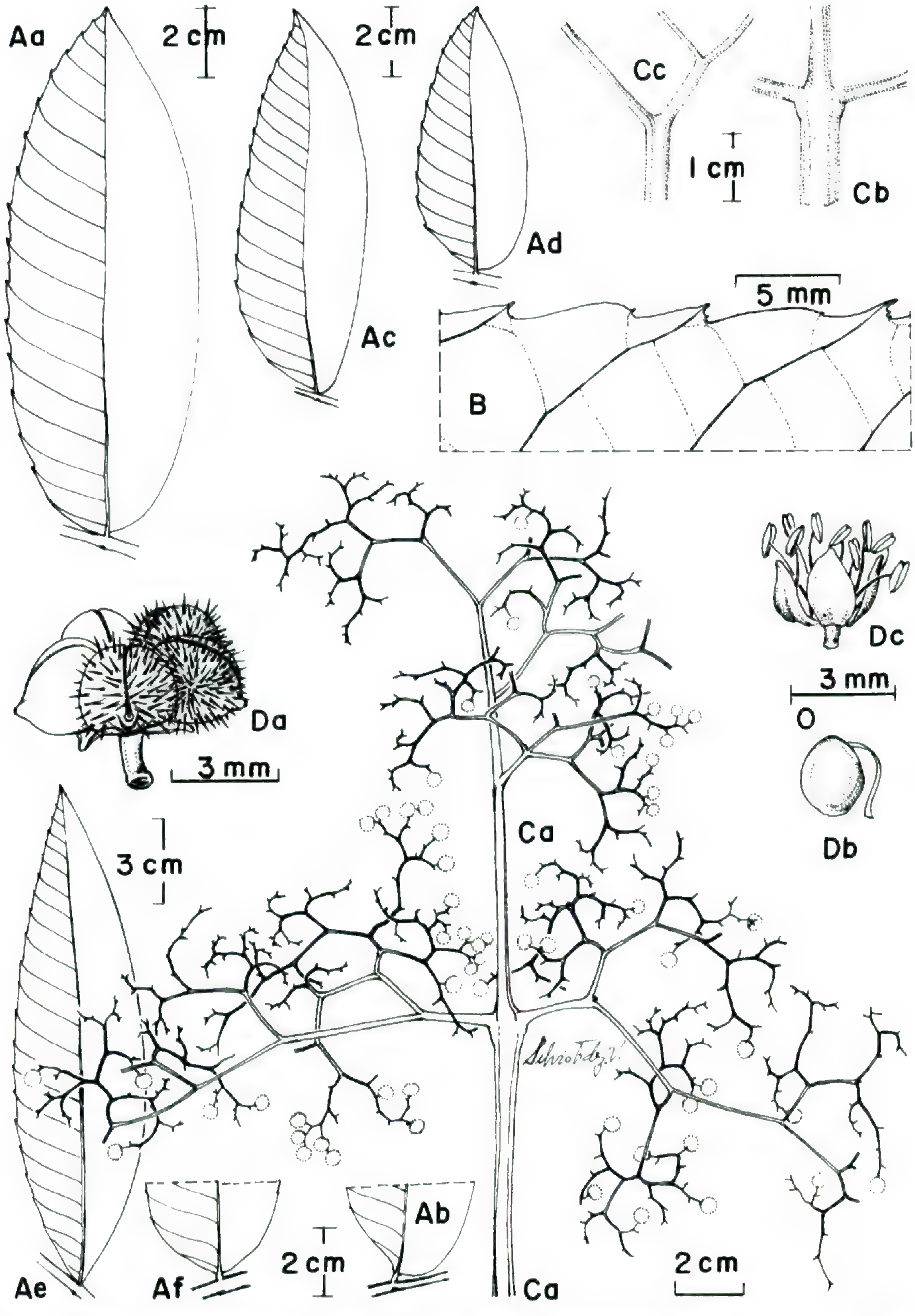


FIGURA 17. *Brunellia comocladifolia* Humb. & Bonpl. subsp. *cundinamarcensis* Cuatrec.—A. Forma, tamaño de los folíolos y estado del pecíolulo.—B. Margen del folíolo.—Ca. Inflorescencia completa.—Cb, Cc. Ramificación de la inflorescencia. D. Partes de la flor y fruto.—Da. Folículos.—Db. Forma de la semilla.—Dc. Flor masculina. A (a, b), C (a–c), y D (a, b), *Orozco et al. 1102*; A (c, d), *Garcia-Barriga 20379*; A (e, f), y D (c), *Orozco et al. 1267*; B, *Orozco et al. 1251*.

2a. Brunellia sibundoya Cuatrec. subsp. **sibundoya** Fl. Neotropica 2: 80. 1970; Supplement 46. 1985. TIPO: Colombia. Comisaría del Putumayo: Cuenca alta del río Putumayo en el Valle de Sibundoy, 2,200 m, 1 ene. 1941 (fr), *Cuatrecasas 11570* (holótipo, US; isótipos, F, US). Figura 18.

Brunellia sibundoya Cuatrec. subsp. *sebastopola*. Fl. Neotropica 2: 81. 1970; supplement 46–48. 1985. TIPO: Colombia. Cundinamarca: cordillera oriental, entre Sebastopol y Alto de las Escaleras, 2,300–2,400 m, 21 mar. 1942 (fl, ♂), *Cuatrecasas 13586* (holótipo, US; isótipos, COL, F).

Arbol 8–20 m. Folíolos sésiles, generalmente

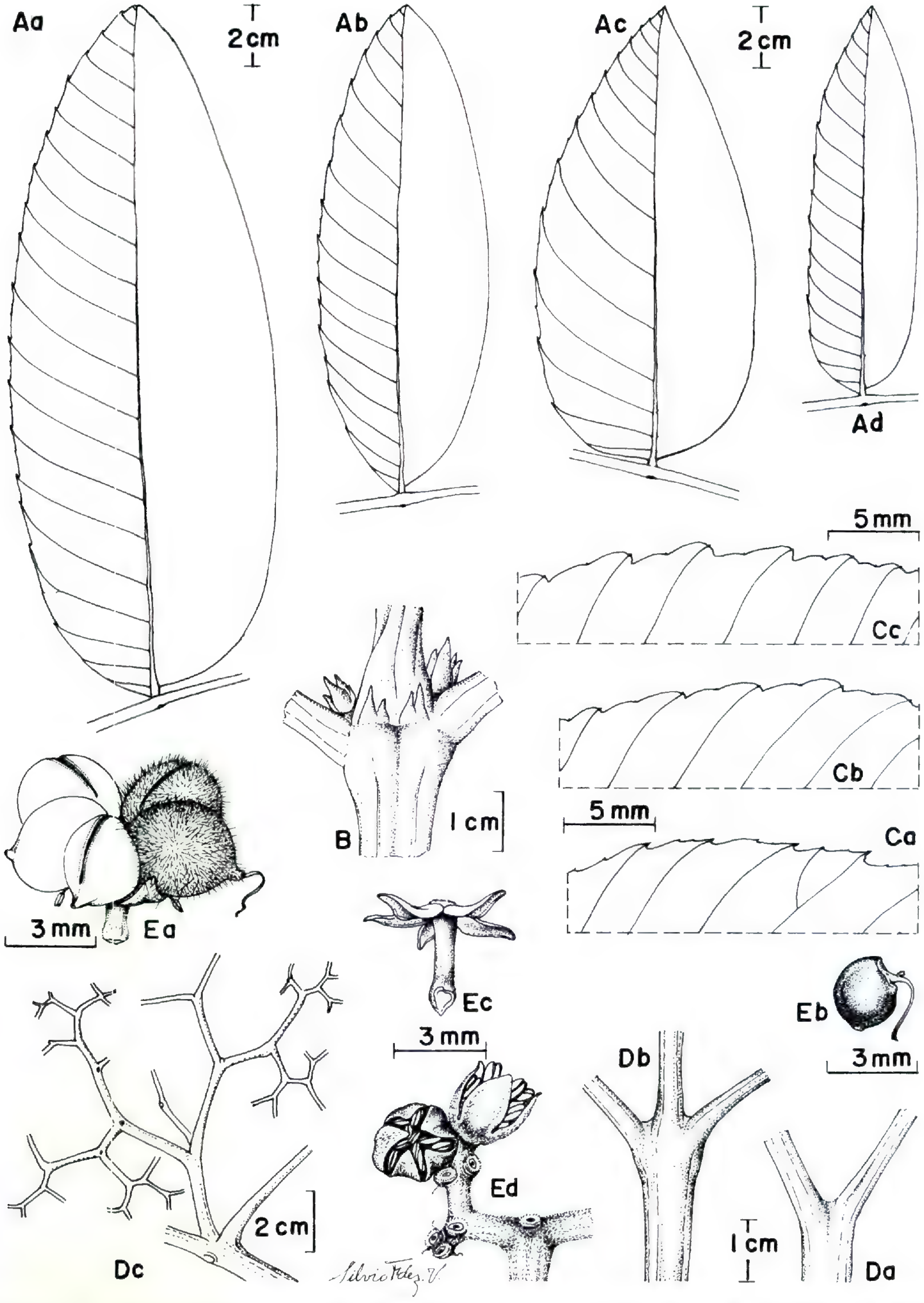


FIGURA 18. *Brunellia sibundoya* Cuatrec. subsp. *sibundoya*.—A. Forma y tamaño de los folíolos.—B. Detalle de las estípulas.—C. Margen del folíolo.—Da, Db. Ramificación de la inflorescencia.—Dc. Inflorescencia completa. E. Partes de la flor y fruto.—Ea. Folículos.—Eb. Forma de la semilla.—Ec. Número de lóbulos del cáliz.—Ed. Flor masculina. A (a), D (a, b), y E (a–c), *Orozco et al. 1273*; A (b), *Cuatrecasas 11570*; A (c), *Schultes 3202*; A (d), *Orozco et al. 239*; C (a), *Vidal 113*; C (b), *Idrobo et al. 10325*; C (c) y E (d), *Cuatrecasas 13586*; D (c), *Bristol 1273*.

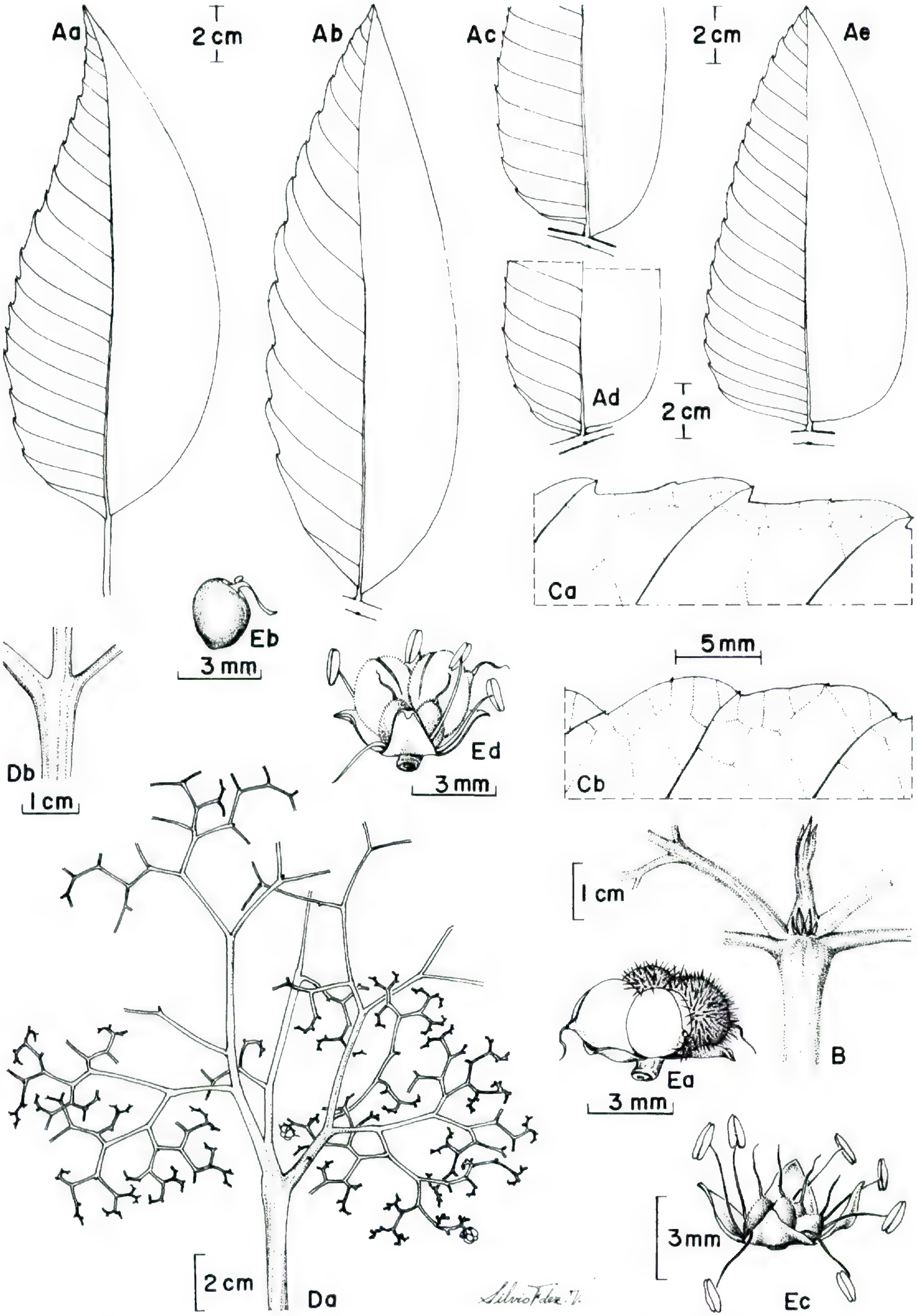


FIGURA 19. *Brunellia sibundoya* Cuatrec. subsp. *antioquensis* Cuatrec.—A. Forma, tamaño de los folíolos y estado del peciólulo (a, folíolo terminal).—B. Detalle de las estípulas.—C. Detalle de la margen del folíolo.—Da. Inflorescencia completa.—Db. Ramificación de la inflorescencia.—E. Partes de la flor y fruto.—Ea. Folículos.—Eb.

crenado-serrados, con menos frecuencia dentados. Cáliz 5–6 lóbulos. Carpelos 5–6. Folículos todos desarrollados. Granos de polen con exina perforada rugulosa.

Distribución. Se registra desde el Macizo colombiana hasta Cundinamarca en la cordillera oriental y para el Tolima en la cordillera central.

Ejemplares representativos. COLOMBIA. CUNDINAMARCA: Municipio de San Francisco, Vereda las Minas, 2,600 m, may. 1981 (fr), *Orozco & Barrera 239* (COL); Municipio de Zipacón, Sebastopol, 2,480 m, 20 nov. 1984 (fr), *Orozco & Carbonó 1273* (COL); cerros de los alrededores de Bogotá, 2,700 m, 11 jun. 1962 (fl, ♂), *Saravia 1207* (COL). TOLIMA: El silencio, Juntas, 2,400 m, 8 dic. 1984 (fr), *Vidal s.n.* (COL); Municipio Santa Isabel, Vereda La Yuca, Alto La Esperanza, 2,700 m, 11 jul. 1980 (fl), *Idrobo, Cleef, Rangel & Salamanca 10325* (COL). PUTUMAYO: Valle de Sibundoy, 2,200 m, 19 jul. 1963 (fr), *Bristol 1247* (COL); 2,250 m, 12 feb. 1942 (fr), *Schultes 3202* (COL).

El isótipo estudiado de *Brunellia sibundoya* subsp. *sebastopola* es un especimen de flores masculinas y folíolos delgados. La condición sésil observada en previos trabajos y utilizada como caracter diagnóstico para diferenciar las subspecies *sebastopola* y *sibundoya* es constante en las inflorescencias masculinas. La condición delgada de los folíolos utilizada también como caracter diagnóstico representa solo un estado de la variación.

2b. Brunellia sibundoya subsp. **antioquensis** Cuatrec. Fl. Neotropica 2: 85. 1970. *Brunellia antioquensis* (Cuatrec.) Cuatrec. Fl. Neotropica 2; Supplement 48. 1985. TIPO: Colombia. Antioquia: Cerca de Santa Elena, entre Medellín y Río Negro, 2,300–2,500 m, (fl, fr), *Gutierrez & Deslisle 1126* (holótipo, F; isótipo, F). Figura 19.

Arbol 6–15 m. Folíolos sésiles o cortamente peciolulados, crenado-serrados o fuertemente dentados. Cáliz 4 lóbulos, menos frecuente 5. Carpelos 4, raro 5. Folículos todos desarrollados. Granos de polen con exina irregularmente reticulada.

Distribución. Se extiende hacia el norte de Colombia en las cordilleras occidental y central (vertiente occidental). Se registra en los departamentos del Valle del Cauca, Caldas, y Antioquia.

Ejemplares representativos. COLOMBIA. ANTIOQUIA: Municipio de Giraldo, carretera a Urabá, Boquerón de Toyo, 2,100 m, 19 mayo 1983 (fr), *Bernal 626* (COL); Municipio de Medellín, cerro del Boquerón, 2,420 m, 29 nov. 1984 (fr), *Orozco, Tobón & Henao 1320* (COL); Municipio de Río Negro, Sajonia, 2,290 m, 27 nov. 1984 (fr), *Orozco, Tobón & Henao 1286* (COL); Municipio de Santa Fé de Antioquia, Cañasgordas, Boquerón de Toyo, 2,000 m, 18 feb. 1985 (fl, ♂), *Henderson & Bernal 145* (COL); Municipio de Urrao, Alto de Caicedo, 2,270 m, 4 dic. 1984 (fl, ♂, fr), *Orozco, Tobón & Henao 1355* (COL). CALDAS: San Antonio de Padua, 2,430 m, 6 oct. 1981 (fl), *Orozco, Rivera, Torres, Pinto & Lozano 259* (COL).

CONCLUSIONES

De los tres taxa considerados al iniciar el estudio sólo dos especies, *Brunellia comocladifolia* y *Brunellia sibundoya*, se reconocen por los análisis de agrupamiento, componentes principales (ACP) y el árbol de la mínima distancia (PRIM). Los dos taxa son el resultado de los estudios de 17 Unidades Taxonómicas Operacionales y 32 caracteres morfológicos.

Los caracteres diagnósticos para reconocer las dos especies son en escaso número. Sin embargo, los taxa son fenéticamente distintos con base en la similitud total de los 32 caracteres. Los caracteres cuantitativos continuos como el ancho de los folíolos, directamente relacionado con la forma (Orozco, 1989), y el grosor de las ramificaciones de las inflorescencias pueden ser considerados como tendencias en el reconocimiento de las especies, mas no como caracteres diagnósticos por presentar superposición de los límites de variación.

Las diferentes interconexiones fenéticas (PRIM) observadas entre las unidades taxonómicas que integran *B. sibundoya*, y los agrupamientos de distancia entre diferentes miembros de las dos subespecies son atribuídas a la variación de los caracteres cuantitativos continuos (24 en total). Posiblemente, la amplia distribución del taxon está relacionada con la plasticidad fenótipica de estos caracteres. Para *B. comocladifolia* se registra una mayor homogeneidad medida por la constante asociación entre las UTO que integran cada una de las subespecies; en otras palabras siempre se encuentran las mismas UTO conformando los grupos infraespecíficos, por otra parte en el PRIM se encuentra sólo una interconexión entre miembros de los dos grupos infraespecíficos.

Mientras que la temperatura en relación con el gradiente altitudinal es un factor determinante para

←
Forma de la semilla.—Ec. Flor con estambres y carpelos poco desarrollados.—Ed. Folículos y estambres. A (a), C (b), D (a), y E (a, b), *Orozco et al. 1286*; A (b) y E (c), *Henderson et al. 145*; A (d), *Orozco et al. 1289*; B, *Orozco et al. 1186*; C (a), *Bernal et al. 626*; D (b), *Orozco et al. 1290*; E (d), *Orozco et al. 1320*.

la diferenciación específica, la humedad es posiblemente para el caso de la variación infraespecífica el factor predominante. Los taxa infraespecíficos con la tendencia hacia el menor número de partes florales están distribuídos en las zonas de mayor humedad, la cordillera occidental y la vertiente occidental de la cordillera central.

Por los datos de distribución se infiere que la diferenciación infraespecífica está muy estrechamente relacionada con la bifurcación de los ramales de la cordillera de los Andes en el Sur de Colombia. Sin embargo, la subespeciación para el caso de *B. sibundoya* se registró hacia el norte de la cordillera central.

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APÉNDICE I. Matriz básica de datos. Información obtenida para cada Unidad Taxonómica Operacional (UTO).

Caracteres	UTO 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	34.95	22.92	31.52	24.50	35.62	45.17	30.84	26 83	29.70	46.30	34.15	31.11	61.50	34.00	57.30	31.93	51.22
2	8.25	4.70	7.06	6.17	7.69	9.84	7.16	9.06	9.59	14.97	9.09	11.11	12.30	7.29	11.36	8.61	13.00
3	12.34	12.68	9.98	9.09	12.01	13.60	12.30	12.30	11.67	19.04	11.51	15.16	17.78	11.53	16.20	9.90	15.24
4	4.80	2.41	3.84	3.16	4.20	4.23	6.44	4.77	4.61	6.90	4.44	5.23	6.71	3.79	6.17	4.61	6.22
5	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
6	1	1	1	2	2	2	2	2	2	1	3	2	2	1	1	1	1
7	5.84	4.83	5.22	4.27	4.03	3.93	6.14	5 42	6.45	6.12	5.40	5.75	5.87	6.59	5.20	5.93	6.61
8	1	1	1	2	2	2	2	N.C	2	1	2	3	2	1	1	1	1
9	8.58	6.36	8.18	6.26	7.01	7.60	8.50	7.12	7.62	10.78	7.21	7.98	9.83	8.41	9.43	8.84	9.05
10	2.55	2.48	2.67	2.00	2.30	1.81	2.24	1.28	1.31	1.26	1.43	1.76	1.65	1.42	0.98	1.38	1.30
11	.56	.36	.86	.80	.50	.56	1.18	1.14	1.24	.88	.88	1.07	N.C	.95	.65	.95	.83
12	3.23	2.80	4.56	2.91	4.98	4.94	4.68	4.25	5.08	8.15	4.23	4.53	6.37	3.25	5.95	4.05	9.87
13	16.25	10.53	28.62	10.36	16.47	18.30	13.84	11. 87	28.65	19.00	13.20	13.73	19 13	12.08	24.50	22.66	9.05
14	2.85	2.90	3.00	2.70	2.75	2.78	3.56	3.03	3.61	3.02	3.19	3.44	3.61	3.11	2.89	3.61	3.33
15	2.58	2.66	2.87	2.68	2.67	2.53	3 36	2.50	3 08	2.70	2.93	3.27	3 48	2.78	2.66	3.47	3.82
16	1	1	1	1	1	1	2	2	2	2	2	N.C	2	2	2	2	2
17	1.75	1.70	1 .61	1.50	1.65	1.62	2.00	2.70	1.62	1.46	UN.C	1.88	1.97	N.C	N.C	1.71	1.88
18	2.03	2.06	1 94	1.96	1.92	2.10	2 37	2.50	2.01	1.99	N.C	2.12	2.26	N.C	N.C	1.95	2.13
19	2.41	2.43	2.15	2.11	2.43	2.43	3.28	2.10	2.03	2.60	N.C	3 .11	3.00	2.91	N.C	2.88	2.96
20	2.27	1.65	1.65	2.40	2.10	2.40	3.27	3.00	2.66	2.43	2.62	3 68	3.20	2.61	3.46	3.53	3.12
21	1.63	1.20	1.20	1.69	1.54	1.72	2.77	2.05	2.04	1.72	2.03	2.97	2.40	1.93	2.25	2.24	2.70
22	.87	.92	1.01	1.00	1.25	1.35	2.07	2.00	1.80	1.62	1.55	2.30	1.99	1.34	1.91	1 83	2.25
23	1	1	1	1	1	1	2	N.C	2	2	N.C	2	2	N.C	N.C	ε	2
24	4.97	3.60	2.63	6.16	8.90	8.67	11.21	8.50	8.61	14.12	7.27	11.74	11.99	7.27	7.45	5.92	944
25	2.57	1.65	1.96	2.63	3.72	3.27	5.67	3.93	3.90	6.12	3.79	4.84	5.70	3.35	3.62	3.78	5.26
26	3.40	2.90	2.49	2.47	N.C	2.90	3.77	N.C	3.16	3.08	5.09	2. 81	4.30	3.02	N.C	N.C	N.C
27	2.31	1.15	2.91	2.58	1.41	2.38	2.68	3.10	2.43	3.12	1.15	3 14	2.30	1.78	3.68	2.70	2.56
28	1 70	1.30	1.18	1. 84	1.20	1.66	2.04	1.55	1.12	1.16	1.08	1.45	1.87	1.99	2.27	2.62	2.15

N.C = No comparable

UTO

Caracteres	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
29	1.05	.85	1.38	1.09	1.12	1.29	1.78	1 81	1 35	1.48	1.10	1.81	1.70	1.58	2.71	1.46	1.86
30	1	1	1	3	2	2	3	3	3	2	3	3	3	2	2	2	2
31	2	2	2	1	1	1	3	3	3	1	1	1	1	3	3	3	3
32	2	2	2	1	1	4	4	4	4	4	4	4	4	3	3	3	3

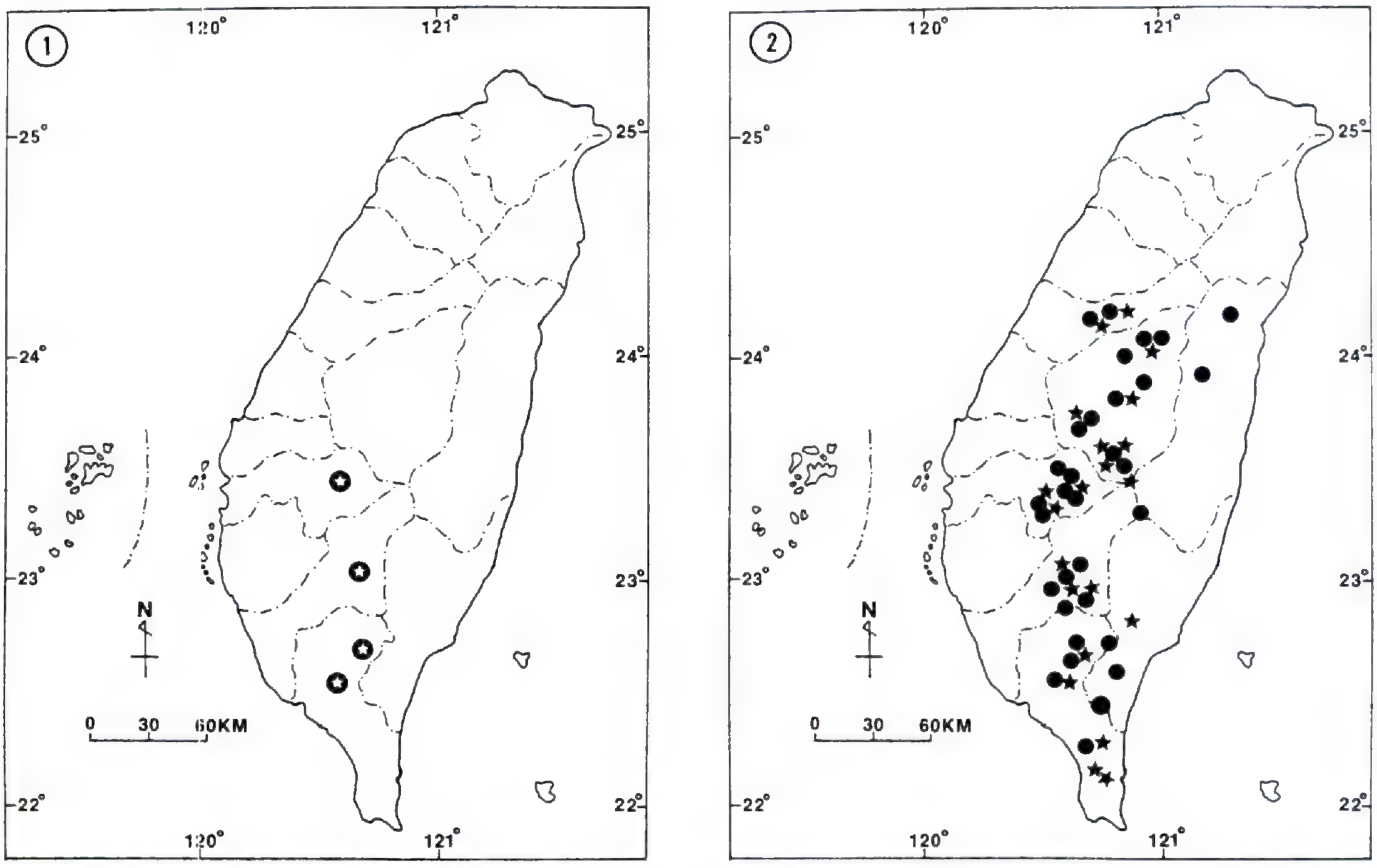
HYBRIDITY AND PARENTAGE OF *BEGONIA BUIMONTANA* YAMAMOTO (BEGONIACEAE) FROM TAIWAN[1]

Ching-I Peng[2] *and Yung-Kuan Chen*[2]

ABSTRACT

Begonia buimontana Yamamoto has been considered an endemic species with a restricted distribution at elevations between 1,000 and 1,600 m in southern Taiwan. Studies of morphology, flowering habit, pollen stainability, and meiotic chromosome behavior suggest a hybrid origin. Morphological comparisons, distribution patterns, chromosome cytology, and experimental hybridization show that *B. buimontana* consists of F_1 hybrids between *B. palmata* D. Don and *B. taiwaniana* Hayata. The hybrid nature and meiotic abnormalities in *B. buimontana* may account for its sterility and explain in part its rarity in nature. A description and line drawing of this hybrid are given.

The genus *Begonia* is represented by ten species in Taiwan (Liu & Lai, 1977; Lai, 1979, 1990; Liu & Ou, 1982; Peng et al., 1988; Peng & Chen, 1990). In our systematic revision of *Begonia* of Taiwan, our attention was drawn to a peculiar habit of *B. buimontana*, an endemic with a restricted distribution at elevations between 1,000 and 1,600 m in southern Taiwan (Fig. 1). We were initially puzzled by not finding any opened staminate flowers in herbarium specimens of this species, although opened pistillate flowers are common. In our field trips to the type locality of *B. buimontana*, we



FIGURES 1 & 2. Distribution maps for Taiwan.—1. *Begonia buimontana*.—2. *Begonia taiwaniana* (stars), and *B. palmata* (dots).

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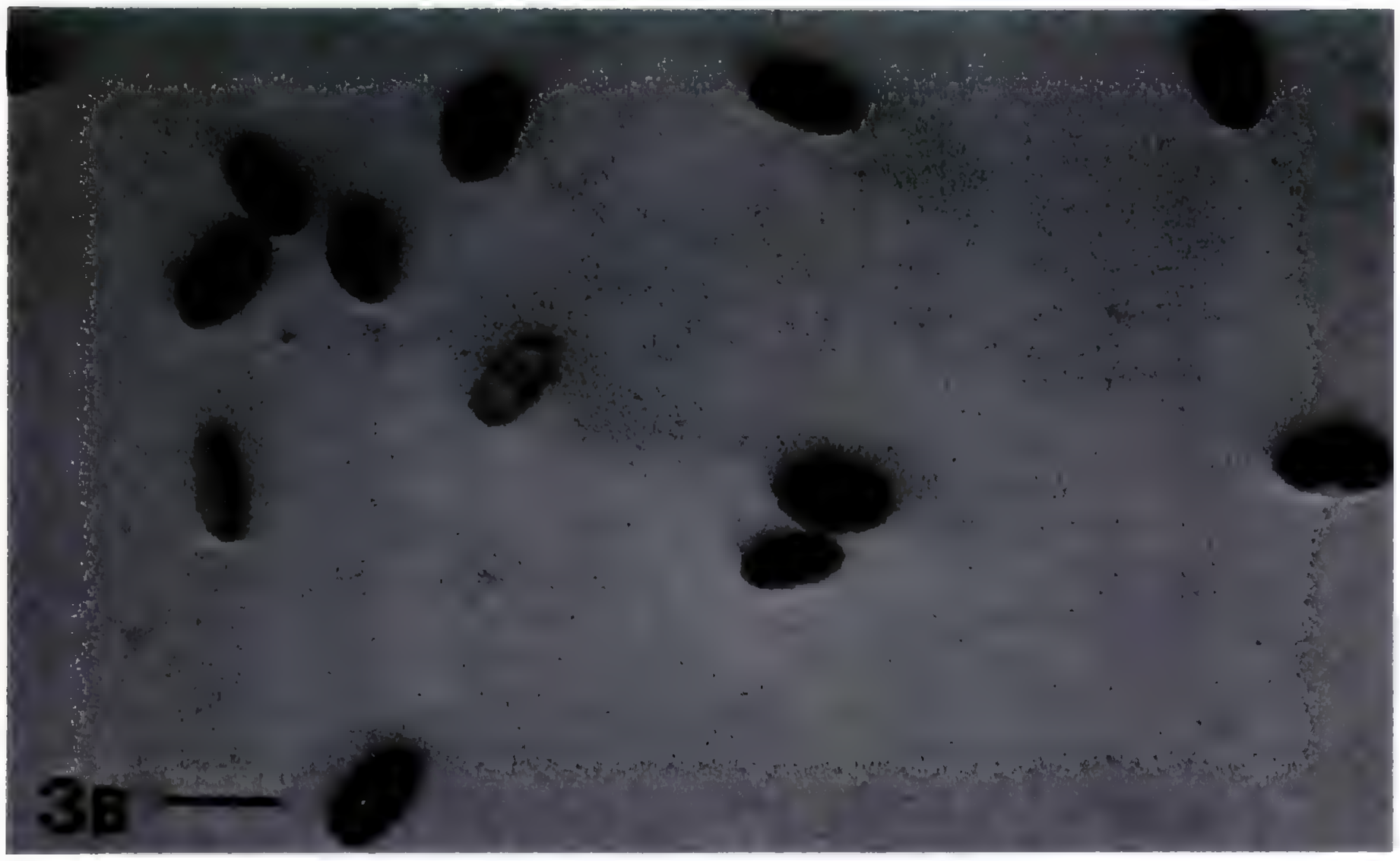
3A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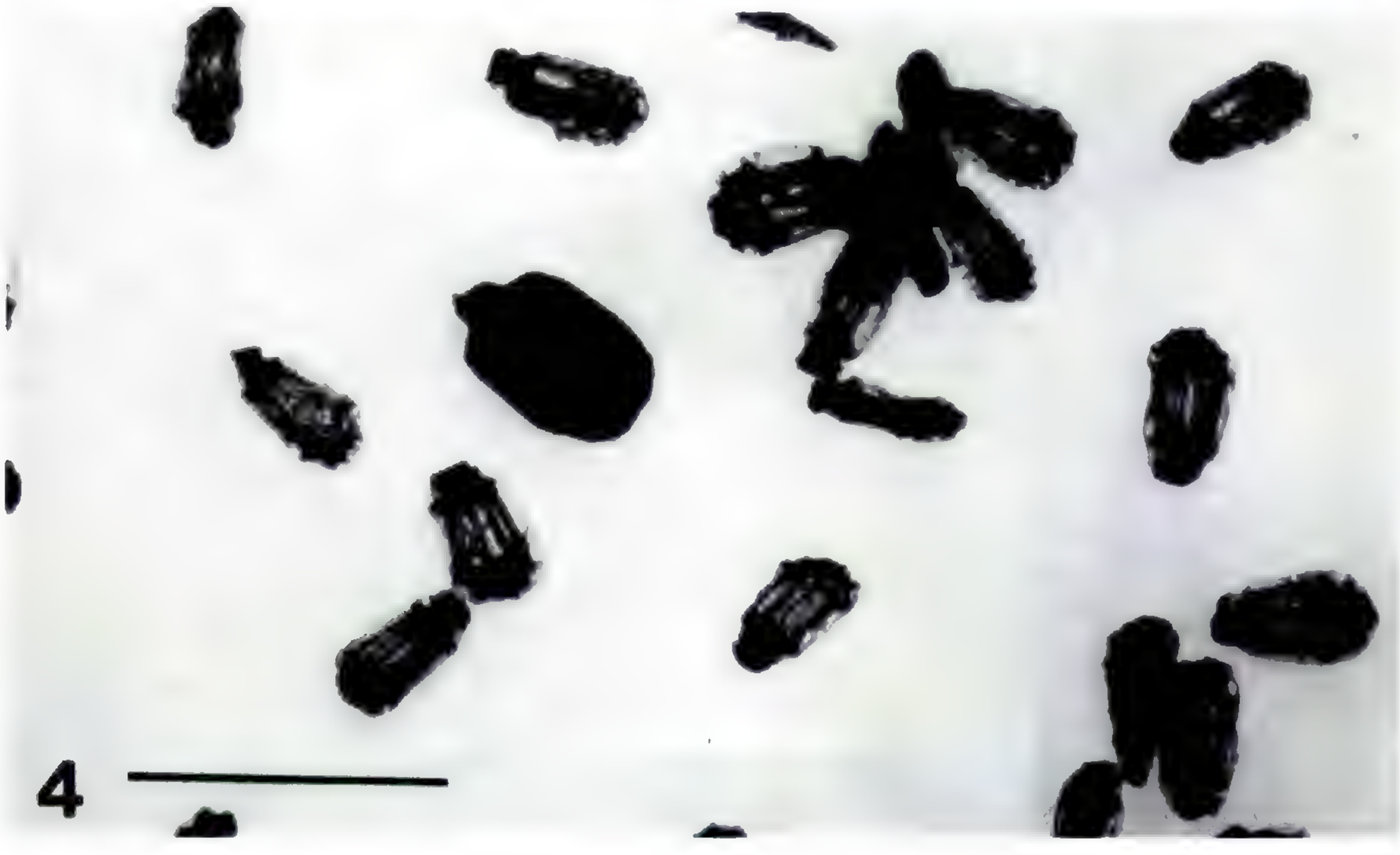
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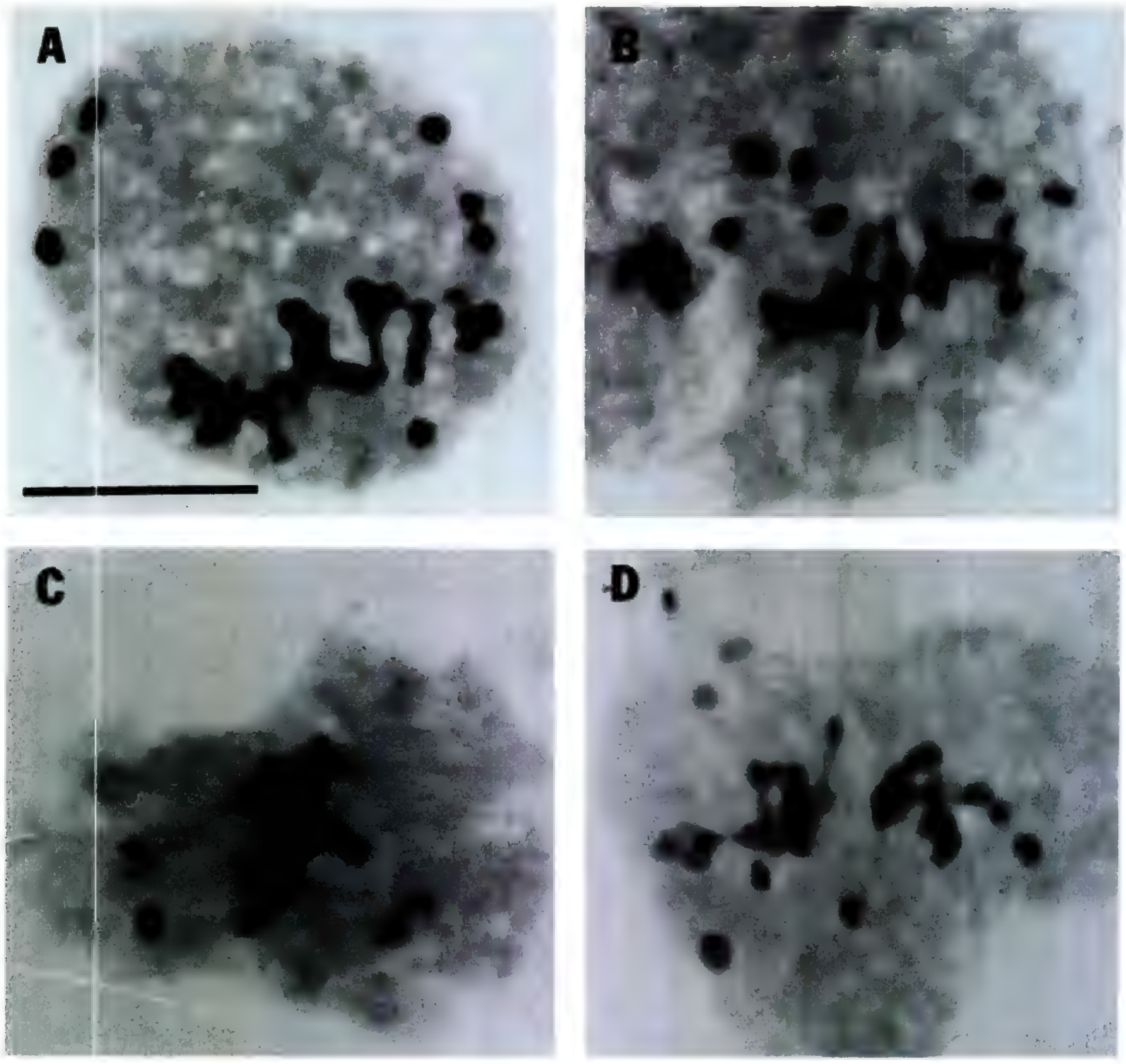

FIGURE 5. Meotic chromosome spreads of *Begonia buimontana*.—A–D. Metaphase I, showing sticky, often disoriented bivalents, univalents, and multivalent associations. All from *Chen 671* (HAST). Bar equals 10 μm.

observed many live plants. Like all other species of *Begonia* in Taiwan, *B. buimontana* is androgynous and produces staminate flowers prior to pistillate flowers. All plants of *B. buimontana* at anthesis produced abundant flowers of both sexes. All staminate flowers observed developed normally up to their late bud stage and dropped off before they were open. By contrast, pistillate flowers were always fully open at anthesis, and bud drop did not occur. Plants brought back from the wild and cultivated in the experimental greenhouse behaved similarly.

Although staminate flowers of *B. buimontana* were shed prematurely, the plants appeared to set abundant fruits. We suspected initially that, in the field, on some plants staminate flowers may open normally to make fruit set possible. An examination of the pollen fertility of *B. buimontana* estimated by determining the percentage of stainable pollen using the malachite green-acid fuchsin-orange G stain of Alexander (1969), however, revealed nearly complete pollen abortion (Fig. 3). Careful examination of mature capsules of *B. buimontana* revealed that, although the fruits were well formed, they contained very few plump seeds (Fig. 4).

Cytological studies showed that *B. buimontana* has a somatic chromosome number of $2n = 30$. Chromosome configurations at meiotic metaphase I typically consisted of some sticky, often disoriented bivalents and up to at least 11 univalents; multivalents are often present (Fig. 5).

The aberrant phenomena led us to suspect a hybrid origin in *Begonia buimontana*. In our search for putative parents, *B. palmata* D. Don and *B.*

←

FIGURE 3. Aberrant and aborted pollen of *Begonia buimontana* (A) vs. mostly normal and stainable pollen of other species of *Begonia*, e.g., *B. taiwaniana* (B). Bar equals 20 μm.

FIGURE 4. A portion of the seeds from a capsule of *B. buimontana*: all but one aborted. Bar equals 0.5 mm.

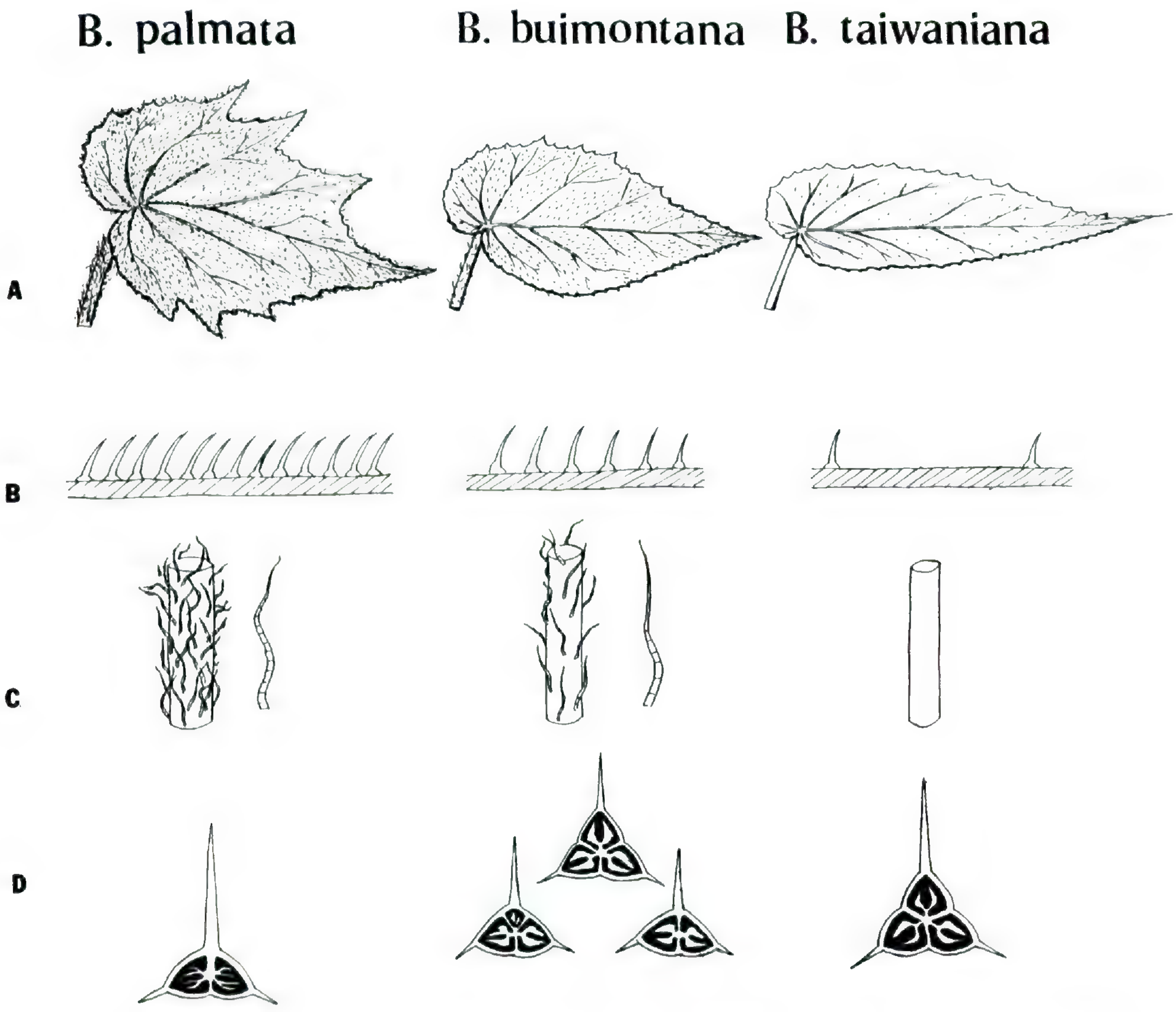

FIGURE 6. Comparison of *Begonia buimontana* with putative parents.—A. Leaf.—B. Leaf, cross section.—C. Petiole and hair type.—D. Fruit, cross section, showing placentation.

taiwaniana Hayata, the only species that commonly associate with *B. buimontana*, came to mind. *Begonia palmata* and *B. taiwaniana* are widespread and sympatric in the mountainous areas of central and southern Taiwan (Fig. 2). An analysis of vegetative and floral characteristics showed that *B. buimontana* is indeed intermediate between *B. palmata* and *B. taiwaniana* (Fig. 6; Table 1). Furthermore, cytological data showed that *B. palmata* has $n = 11$ and *B. taiwaniana* has $n = 19$; a somatic chromosome number of $2n = 30$ would be expected in F_1 hybrids of the two species (Fig. 7).

In order to substantiate our hypothesis that *B. buimontana* is derived from natural hybridization between *B. palmata* and *B. taiwaniana*, we crossed the putative parents and obtained artificial F_1 hybrid plants. These plants closely resembled *B. buimontana* in aspect and morphology. Furthermore, as in wild plants of *B. buimontana*, they shed staminate flowers precociously. They have a somatic chromosome number of $2n = 30$ and negligible stainable pollen, too.

In conclusion, we consider that *B. buimontana* from Taiwan represents a hybrid, which, as a result of discrepancy in chromosome number and/or disharmony in genomes of the parental species, is pollen sterile and sheds staminate flowers prematurely. Plants of *B. buimontana* brought back from the field flowered in the insect-free experimental greenhouse but failed to set fruit. By contrast, mature fruits with a few seeds were often observed in plants of *B. buimontana* in the field. These were probably derived from back crosses with the putative parental species. Some of these seeds germinated in the experimental greenhouse but died at the cotyledonous stage.

Although both putative parents are widespread and sympatric in the mountainous areas of central and southern Taiwan, (Fig. 2), *B. buimontana* is

TABLE 1. Comparison of *Begonia buimontana* with putative parents.

Characters	*B. palmata*	*B. buimontana*	*B. taiwaniana*
Creeping rhizome	present	lacking	lacking
Plant height (cm)	to 60	to 100	to 200
Leaf width : length ratio	1 : 1–1.5	1 : 2–2.5	1 : 3–4.5
Pubescence	Densely scabrous	Scabrous	Sparingly scabrous to nearly glabrous
Number of styles	2	3	3
Number of ovary cells	2	(2–) 3	3
Length of abaxial wing of capsule (cm)	ca. 2	ca. 1	ca. 1
Chromosome number	$n = 11$	$2n = 30$	$n = 19$

known only from the type locality (Yamamoto, 1933) and three other stations (Fig. 1). Recently, Ying (1988) described *Begonia fenchihuensis*. An examination of his original description and type specimens reveals that it is synonymous with *B. buimontana*. The type locality of *B. fenchihuensis* represents the northernmost station known for *B. buimontana*. In this study we collected *B. buimontana* from two additional localities (Fig. 1 and see below).

Although *B. buimontana* is relatively rare on Taiwan, plants of this hybrid were fairly abundant where found, frequently intermixing with both putative parents, at least in the three localities we visited. The physiological characteristics and ecological tolerances of the putative parents may have recombined in the hybrids in such a way as to limit its distribution range.

Begonia buimontana is most likely represented only by F_1 hybrids. Populations are very uniform morphologically, and experimental F_1 hybrids are comparable to wild plants. Although such hybrids are sterile, once established, they are able to persist in a given location due to their perennial habit. The expansion of their populations on the island, however, can only be achieved by recurrent natural hybridizations.

The taxonomic treatment and an illustration of this hybrid species are given below.

Begonia ×buimontana Yamamoto (pro sp.), J. Soc. Trop. Agric. 5: 353. 1933. Liu & Lai in Li et al., Fl. Taiwan 3: 792. 1977. TYPE: Taiwan. Pingtung County ("Hsien"): Wuweishan. *Matuda 322* (holotype, TAI). Figure 8.

Begonia fenchihuensis Ying, syn. nov. Color Ill. Fl. Taiwan 3: 618. 1988. TYPE: Taiwan. Chiayi County ("Hsien"): Fenchihu to Shihcho (as Shi-Chao), elev. 1,400 m, 16 Jan. 1988, *S. S. Ying s.n.* (holotype, Herb., Dept. Forest., Natl. Taiwan Univ.; isotype, Herb., Dept. Forest., Natl. Taiwan Univ.)

Erect, perennial, succulent herb; horizontal rhizomes lacking. Stems glabrous or sometimes remotely pilose, 40–125 cm high, to 26 mm diam. Stipules glabrous, caducous, ovate to broadly ovate, to 23 mm long, 18 mm wide, the apex acuminate, the margins entire. Leaves densely scabrous or hirsute on both surfaces, obliquely lanceolate to narrowly ovate, 8–22 cm long, 4–8 cm wide, the apex acuminate to cuspidate, the base obliquely cordate, the margins irregularly denticulate or serrulate; venation palmate, the veins 5–8, sometimes

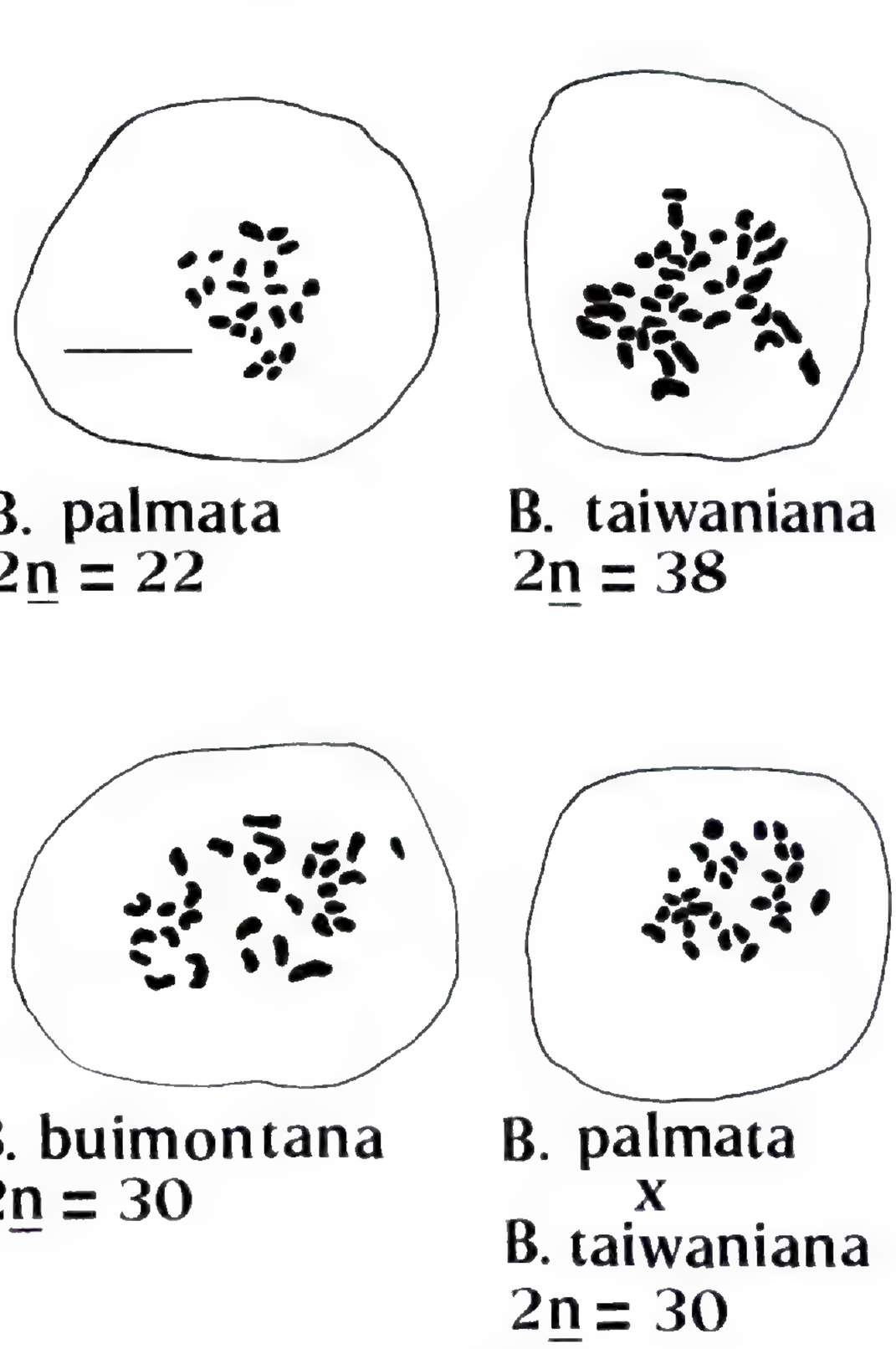

FIGURE 7. Camera lucida drawings of somatic chromosome spreads of *B. palmata*, *B. taiwaniana*, *B. buimontana*, and an experimental hybrid, *B. palmata* × *B. taiwaniana*. Bar equals 10 μm.

FIGURE 8. *Begonia* ×*buimontana*.—A. Habit.—B. Bract.—C. Stipule.—D. Stamen.—E. Pistillate flower.—F. Staminate flower, from a bud opened and spread with a forcep.—G, G′. Style.—H. Fruit, external morphology.—I, I′, I″. Fruit, cross section, showing placentation.—J. Seed.

villous; petioles rusty villose, 7–16 cm long, to 5 mm diam. Bracts in pairs, thickly papery, glabrous, caducous, narrowly ovate to ovate, to 24 mm long, 17 mm wide, the apex mucronate to acuminate, the margins entire. Inflorescence 6–11 cm long; peduncles erect to pendulous, glabrous or sometimes pilose, to 7 cm long, 2 mm diam. Flowers pink, abaxial surfaces of the outer tepals densely scabrous. Staminate flower: tepals 4, never open, the outer two obovate to orbicular, to 14 mm long, 13 mm wide, the inner two oblanceolate to narrowly obovate, to 13 mm long, 6 mm wide; stamens numerous, to ca. 140, some of which may be reduced, yellow, golf-club-shaped, the anthers narrowly obovoid, 1.8–2.2 mm long, 0.9–1.2 mm across, the filaments 1.5–2.8 mm long. Pistillate flower: tepals 5(–6), unequal to subequal, oblanceolate to orbicular, the largest 11–19 mm long, 9–18 mm wide, the smallest 9–17 mm long, 4–9 mm wide; styles 2–3, yellow, 4.7–5.3 mm long, at their base fused ca. 1.4 mm long, each bifid; ovary inferior, ellipsoid, (2–)3-locular, longitudinally shallowly grooved between the locules, 3-winged; placentae axile, bilamellate. Infructescence to 17 mm long, the fruit-bearing stipes 18–34 mm long; the abaxial wing triangular, 12–19 mm long, 11–16 mm wide, the lateral wings much narrower, 4–6 mm long, 10–14 mm wide. Well-formed seeds few, never exceeding 35 per mature fruit, broadly ellipsoid, 0.35–0.38 mm long, 0.19–0.22 mm thick, the apex rotund, the seed lip nipple-shaped, the micropylar end constricted.

Distribution. Southern part of the Central Mountain Range of Taiwan, at elevations between 1,000 and 1,600 m. Known from Pingtung, Kaohsiung, and Chiayi counties.

Additional specimens examined. TAIWAN. KAOHSIUNG CO.: Tengchi, *Chen & Peng 363* (HAST), *Chen 726* (HAST). PINGTUNG CO.: mountain-hiking entrance of Peitawushan, *Peng 10617, 13240* (HAST), *Chen 644, 662* (HAST), *Lai 9819* (TAI); en route from Peitawushan to Taiwu, *Chen 671, 672* (HAST).

Begonia ×*buimontana* consistently has 5(–6) tepals in pistillate flowers. The report of Liu & Lai (1977) of two pistillate tepals in this hybrid species was incorrect. In Taiwan, the only species of *Begonia* with two tepals in pistillate flowers is *B. ravenii* Peng & Chen (Peng et. al., 1988).

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CARAIPA (GUTTIFERAE) DEL PERU[1]

Rodolfo Vásquez M.[2]

Resumen

Colecciones recientes de *Caraipa* de la Amazonía peruana elevan el número de especies conocidas para el país de tres a ocho. *Caraipa jaramilloi* y *C. utilis* son especies nuevas, y ésta última es la madera de construcción mas importante en Iquitos.

Abstract

Recent collections of *Caraipa* from Amazonian Peru raise the number of species known from that country from three to eight. *Caraipa jaramilloi* and *C. utilis* are new to science, the latter currently the most important construction timber in Iquitos.

Caraipa es un género casi desconocido para el Perú debido en mayor parte a la falta de colecciones en la región amazónica. El presente trabajo reporta ocho especies de *Caraipa* de las cuales tres están en el estudio de Kubitzki (1978), y cinco son nuevas para el Perú, incluyendo dos hasta ahora inéditas. Las ocho especies ahora conocidas para el país están aquí distinguidas por una clave, y solo se describen las especies nuevas; he observado todas las especies menos *C. myrcioides* en el campo, y las descripciones incluyen características de la planta viva además de las de herbario, algunas notas de ecología, nombres vernaculares, y usos de las especies también están incluidos.

Las especies peruanas de *Caraipa* se caracterizan por falta de aletas; fuste cilíndrico; corteza externa generalmente blanca parduzca con escazo ritidoma en placas (en *C. utilis* marrón oscuro o negro); corteza interna rosada o rojiza de textura ligeramente fibrosa, con látex amarillento viscoso o amarillo fluido, u oleoso transparente; y xilema diferenciado semiduro, semipesado con albura rosada, duramen rojizo, textura media, y grano recto.

Caraipa habita casi todos los tipos de bosques primarios de la Amazonía peruana; pero cada especie está ecológicamente restringida a un solo tipo de suelo, un buen ejemplo de la β-diversidad que caracteriza a muchas plantas leñosas de la Amazonía (Gentry, 1981, 1986). Dos especies pueden vivir juntas como *C. utilis* y *C. tereticaulis* que habitan suelos infértiles de arena blanca, o como también *C. jaramilloi* y *C. myrcioides* que habitan suelos arcillosos-arenosos o arcillosos y relativamente fértiles.

Por lo general *Caraipa* tiene madera resistente al ataque de insectos y hongos xilófagos, razón por la que los fustes de casi todas las especies se usan como madera redonda para la construcción de viviendas, tanto en las áreas rurales como en las ciudades, llegándose a comercializar en Iquitos, bajo ésta modalidad a: *C. utilis*, *C. tereticaulis*, y *C. densifolia* subsp. *densifolia* (Vásquez, 1987). Cerca del 70% de la madera redonda que se usa para construcción de viviendas en la zona de Iquitos viene de la primera especie (Perú, 1986).

También es importante destacar el gran valor ecológico de *C. utilis* y *C. tereticaulis* como protectores de los suelos de arena blanca.

Las características del género, respectivas sinonimias de las especies, distribución, y otros usos no se presentan, porque están bien detallados en Kubitzki (1978).

Clave de Especies y Subespecies de *Caraipa* Reportadas para el Peru

1a. Envéz de las hojas pubescente, con células epidérmicas protuberantes, buliformes; cápsulas tomentosas o glabras, trígonas-piramiformes, simétricas o ligeramente curvadas.
2a. Pelos estrellados sésiles y pedunculados; hojas (12–)16–28(–40) cm de longitud; cápsulas tomentosas (2.5–)3–4.2 cm de longitud ... *C. grandifolia* subsp. *grandifolia*
2b. Pelos estrellados sésiles; hojas hasta 21 cm de longitud; cápsulas glabras o con diminutos pelos estrellados muy dispersos, hasta 2.4 cm de longitud.
3a. Hojas elíptico-ovadas u oblongas, 5–12.5 cm de longitud, ápices redondeados u obtusos y frecuentemente

[1] Realizado, dentro del programa de actividades del Proyecto Flora del Perú con la supervisión del A. Gentry.
[2] Proyecto Flora del Perú, Apartado 280, Iquitos, Perú.

emarginados; cápsulas 1.1–1.4 cm de longitud ..... *C. tereticaulis*

3b. Hojas ovado-lanceoladas o lanceoladas, (10–)14–21 cm de longitud ápices agudos y frecuentemente acuminados; cápsulas 1.6–2.4 cm de longitud ..... *C. punctulata*

1b. Envéz de las hojas glabro o glabrescente, sin células epidérmicas protuberantes; cápsulas tomentosas, trígonas-oblicuas, trígonas-subglobosas, o trígonas-ovoides, asimétricas.

4a. Filotaxia en espiral, hojas coriáceas, elípticas ovadas a ovadas, 5–8(–10) cm de longitud; cápsulas trígonas-oblicuas o trígonas-subglobosas 1.5–2.0 cm de longitud ..... *C. utilis*

4b. Filotaxia dística, hojas cartáceas o subcoriáceas lanceoladas u ovadas-lanceoladas, 5.5–18(–20) cm de longitud; cápsulas trígonas-oblicuas, trígonas subglobosas, o trígonas-ovoides.

5a. Hojas 13–18(–20) cm de longitud, venación terciaria subparalela conspicua; cápsulas trígonas-oblicuas o trígonas-subglobosas 3.0 cm de longitud ..... *C. valioi*

5b. Hojas 5.5–14 cm de longitud, venación terciaria subparalela o reticulada inconspicua; capsulas trígonas-oblicuas, trígonas-subglobosas, o trígonas-ovoides, hasta 2.0 cm de longitud.

6a. Inflorescencia vistosa con muchas flores, venación terciaria subparalela cápsulas trígonas-oblicuas, trígonas-subglobosas, o trígonas-ovoides, 1.7–2.0 cm de longitud ..... *C. densifolia* subsp. *densifolia*

6b. Inflorescencia poco vistosa con pocas flores, venación terciaria reticulada; cápsulas trígonas-oblicuas, 1.5–1.8 cm longitud.

7a. Panículas con las ramas laterales bien formadas, pedicelos 4–6 mm de longitud; base de las hojas obtusas, pecíolos 3–4 mm de longitud ..... *C. jaramilloi*

7b. Paniculas con las ramas laterales reducidas a glomérulos con 4–8 flores, pedicelos 1–2 mm long; base de las hojas agudos, pecíolos 5–10 mm de longitud ..... *C. myrcioides*

ESPECIES NUEVAS DE *CARAIPA* REPORTADAS DEL PERU

Caraipa jaramilloi Vásquez, sp. nov. TIPO: Perú. Loreto: Provincia de Maynas, Distrito de Iquitos, Puerto Almendras, bosque primario no inundable, *Vásquez 6528* (holotipo, AMAZ; isotipos, MO, USM, F, G). Figuras 1, 3.

Arbor, 20 m alta. Foliis lanceolatis vel ovato lanceolatis, 6–12 cm longis, 2–4 cm latis; petiolis glabris 3–4 mm longis. Inflorescentia terminales vel laterales, paniculatae, 6–9 cm longis; bracteis bracteolisque lanceolatis caducis; pedicellis tomentosis, 4–6 mm longis; sepalis basi connatis. Capsulis trigonis obliquos 1.5–1.8 cm longis, puberulis, pilis parvis stellatis mayoribusque simplibus praeditis, exocarpio ex endocarpio secedente.

Arbol mediano 20 m de alto, fuste con látex amarillento muy viscoso de lenta segregación, cerca del cambium ligeramente rosado. Ramitas pubescentes o glabrescentes. Hojas dísticas, subcoriáceas, haz glabro, envéz glabro y liso, sin células epidérmicas protuberantes; lanceoladas a ovado-lanceoladas, 6–12 cm de longitud, 2–4 cm de ancho, ápice agudo, generalmente atenuado o terminando en acúmen de 5–10 mm de longitud, base obtusa; nervadura media con escaza pubescencia en el envéz, impresa en la haz, y prominente en el envéz, nervios secundarios 10–12(–14) pares, terciarios reticulados inconspicuos; márgen plano o ligeramente revoluto; puntos translúcidos no visibles o dificilmente visibles; pecíolo glabro, raro pubescente, 3–4 mm de longitud. Inflorescencia terminal o lateral, panículas de 6–9 cm de longitud, raquis, ramitas, pedicelos, y brácteas tomentosas ferrugíneas con pelos simples; brácteas y bractéolas caducas, lanceoladas; bractéolas 1.5–2.0 mm de longitud; pedicelos 4–6 mm de longitud. Yemas florales antes de la antesis globosas 4–6 mm de longitud. Sépalos unidos en la base, con los lóbulos triangulares, 0.8–1.0 mm de longitud por 1.0–1.3 mm de ancho, con los bordes ciliados, tomentosos por fuera, y pubescentes por dentro. Pétalos oblongos con un borde ciliado, tomentosos por fuera y glabros por dentro, 5–8 mm de longitud, por 3.5 mm de ancho. Ovario densamente pubescente hirsuto, 1 mm de longitud, por 1.7 mm diám., estilo 1 mm de longitud. Cápsula trígona-oblicua, curva, contraída en el ápice, 1.5–1.8 cm de longitud, hasta 1.2 cm de ancho en la base, superficie ligeramente rugosa, puberulenta, con pelos ± hirsutos caducos de 0.3 mm de longitud; exocarpo separable del endocarpo; 1–2 semillas por fruto.

Paratipo. PERU. LORETO: Provincia de Maynas, Distrito de Iquitos, Allpahuayo, bosque primario no inundable, *Grández 682* (AMAZ).

Ecología. Bosque primario no inundable, con suelos arcillosos-arenosos o arcillosos, relativamente ricos en nutrientes; florece en noviembre y frutifica en mayo.

Nombre vernacular. Localmente se conoce con el nombre *brea caspi de altura.*

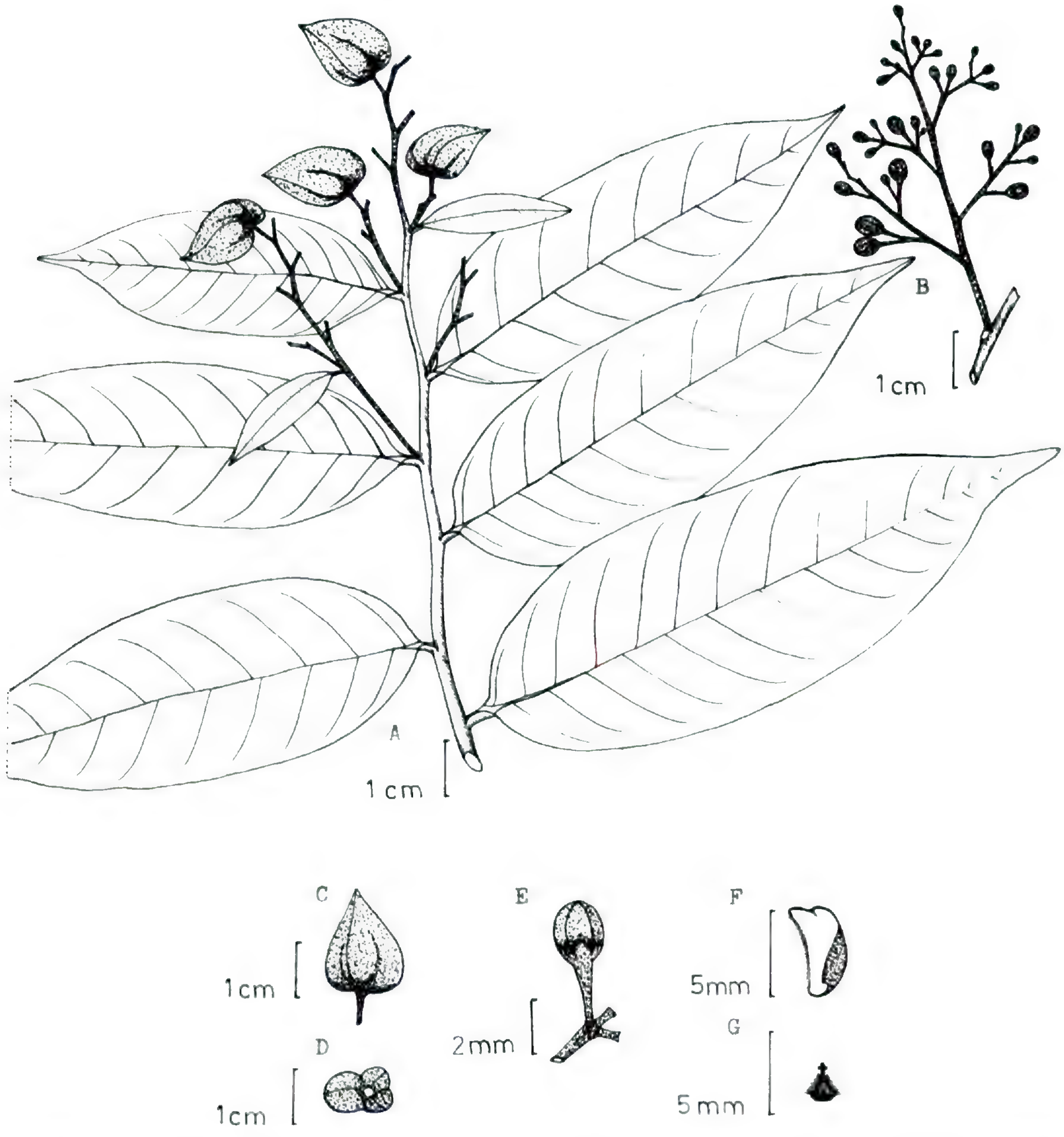

FIGURA 1. *Caraipa jaramilloi* Vásquez. —A. Hábito. [*Vásquez 6528* (AMAZ, MO, USM, F, G).]—B. Inflorescencia. [*Grández 682* (AMAZ).]—C, D. Fruto visto por un costado y por la base respectivamente.—E. Yema floral.—F. Pétalo.—G. Ovario.

Usos. Los fustes se usan como madera redonda, para la construcción de viviendas rústicas.

Caraipa jaramilloi difiere de las otras especies por hojas con venación reticulada inconspicua, bases obtusas, y pecíolos 3–4 mm de longitud y por inflorescencias poco vistosas. Las cápsulas trígonas oblicuas, asimétricas, y tomentosas son similares a las de *C. densifolia* subsp. *densifolia* pero menos robustas, más contraídas, y con pelos simples dispersos; el látex amarillento viscoso, también se asemeja al de ésta subespecie.

Caraipa utilis Vásquez, sp. nov. TIPO: Peru. Loreto: Provincia de Maynas, Distrito de Iquitos, Puerto Almendras, bosque primario no inundable, con suelos de arena blanca, *Vásquez 5543* (holotipo, AMAZ; isotipos, MO, USM, F, G). Figuras 2, 3

Arbor 25 m alta. Foliis spiralibus, ovatis vel ellipticis-ovatis, coriaceis, glabris, 5–8(–10) cm longis, 2.3–4.2 cm latis; petiolis glabris 6–10 mm longis. Inflorescentias terminales vel laterales, paniculatae 6 cm longis, bracteis bracteolisque caducis; pedicellis 5–10 mm longis, glabris.

FIGURA 2. *Caraipa utilis* Vásquez.—A. Hábito. [*Vásquez 5543* (AMAZ, MO, USM, F, G).]—B. Flor (×2).—C. Pétalo (×2).—D. Estambre (×12).—E. Ovario (×6).—F, G. Frutos vistos por un costado y por la base respectivamente. [*Vásquez 6144* (MO, AMAZ, USM).]—H. Hojas de árboles juveniles.

Capsulis trigonis obliquos, ferrugineo tomentellis 1.5–2.0 cm longis, exocarpio ex endocarpio secedente.

Arbol mediano a grande, 25 m de alto, fuste negruzco con ritidoma en placas pequeñas, látex transparente oleoso con puntos blancos. Ramitas glabras, en jóvenes las ramitas puberulentas. Hojas en espiral, coriáceas, haz glabro, envéz glabro y liso, sin células epidérmicas protuberantes; ovadas a elípticas-ovadas, 5–8(–10) cm de longitud, 2.3–4.2 cm de ancho, ápice redondeado o con pequeño acúmen obtuso de 3 mm long, rara vez emarginado, base aguda o a veces obtusa; nervadura media algunas veces escazamente pubérulas en el envéz, impresa en la haz y prominente en el envéz, secundarias 5–7(–9) pares, terciarias subparalelas, visibles en ambos lados; márgen ligeramente revoluto; puntos translúcidos visibles solo en las hojas de los individuos jóvenes; en éstos las hojas hasta 17 cm de longitud, 5.5 cm de ancho, lanceoladas, abruptamente acuminadas 1.5 cm long, base aguda, con 11 pares de venas secundarias; pecíolo glabro, 6–10 mm de longitud. Inflorescencia terminal y lateral, panículas o racimos de 6 cm de longitud, raquis, ramitas, pedicelos, y brácteas glabras; brácteas y bractéolas caducas; pedicelos ro-

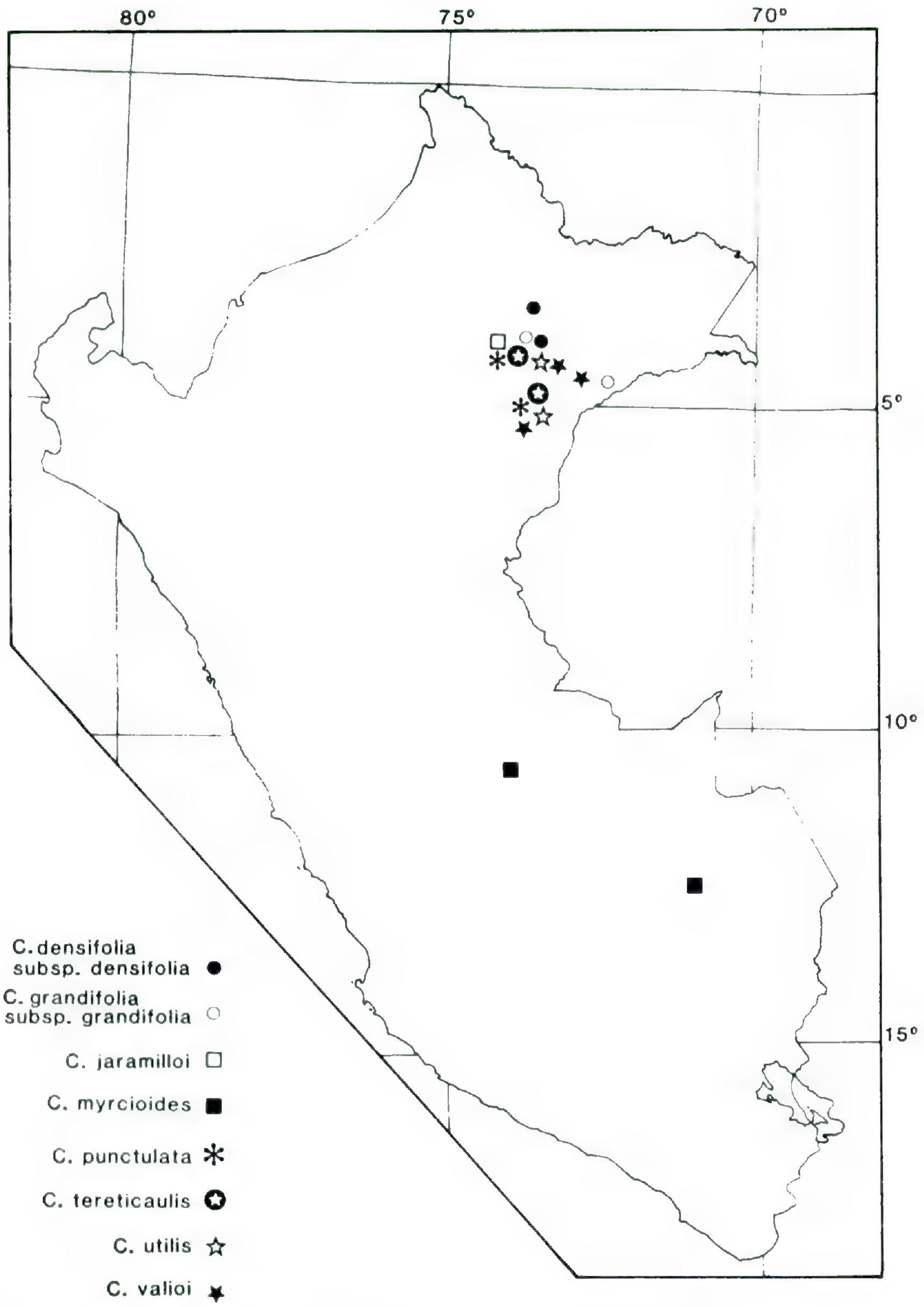

FIGURA 3. Distribución de las especies y subespecies de *Caraipa* en el Perú.

bustos y engrosados hacia el ápice, de 5–10 mm de longitud. Yemas florales antes de la antesis ovoides, 6–7 mm de longitud. Sépalos obtusos, glabros por fuera y pilosos por dentro, ciliados en el borde, lóbulos libres 2.5 mm de longitud, 3 mm de ancho en la base. Pétalos oblongos puberulentos por fuera y uno de los bordes ciliado, hasta 1 cm de longitud, 4–6 mm de ancho. Ovario tomentoso, surcado longitudinalmente, 1 mm de longitud, 0.8 mm diám., estilo 1 mm long. Cápsula trígona-oblicua o trígona-subglobosa, contraída en el ápice en un mucrón de 1 mm de longitud, la cápsula 1.5–2.0 cm de longitud, 1.2–1.5 cm de ancho en la base, superficie, ligeramente rugosa, cubierta con tomento marrón, exocarpo separable del endocarpo, 1(–2) semillas por fruto, ovoides aplanadas 1.7 cm de longitud.

Muestras adicionales examinadas. PERU. LORETO: Provincia de Maynas, Distrito de Iquitos, Mishana, bosque primario no inundable, suelos con arena blanca, *Vásquez 6144* (AMAZ, MO, USM); Maynas, Puerto Almendras, *Vásquez 5518, 5544* (MO, AMAZ, USM); Requena, Jenaro Herrera, *Vásquez 9986* (MO, AMAZ, USM).

Ecología. Bosque primario no inundable, con suelos de arena blanca, algunas veces de extrema infertilidad, comportándose como gregaria, con individuos de reducido diámetro, formando un bosque llamado localmente *varillal*, que es un poco más

alto que el formado por *C. tereticaulis*. Florece en septiembre, y frutifica en enero.

Nombres vernaculares. Localmente se conoce con los nombres siguientes: *aceite caspi*, *aceite caspi colorado* y *aceite caspi negro*.

Usos. Los fustes se usan como madera redonda para la construcción de viviendas, tanto en las áreas rurales como en las ciudades, llegándose a comercializar en gran cantidad, bajo ésta modalidad en Iquitos, también se asierra.

Caraipa utilis difiere de las otras especies por las hojas ovadas a elípticas-ovadas, en espiral, muy coriáceas, aunque las hojas de los individuos jóvenes son difíciles de separar de las de *C. densifolia* subsp. *densifolia*. A diferencia de las otras especies peruanas tiene las inflorescencias glabras; las cápsulas trigonas-oblicuas o trígonas-subglobosas, asimétricas y tomentosas (no son tan pequeñas y contraídas como las de *C. densifolia* subsp. *densifolia*, ni tan grandes como las de *C. valioi*); el látex transparente oleoso con puntos blancos contrasta con el las otras especies; y su preferencia por habitar en bosques con suelos de arena blanca.

Otras Especies de *Caraipa* Reportadas del Peru

Caraipa densifolia subsp. *densifolia* Mart.

Látex amarillo viscoso. Hojas dísticas glabras subcoríaceas, envéz liso, sin células epidérmicas protuberantes. Cápsula tomentosa, trígona-oblicua, trígona-subglobosa, o trígona-ovoide. Habita suelos inundables estacionales por aguas negras, llamados localmente *tahuampas*. Florece en mayo, y frutifica en septiembre. A esta especies se conoce localmente con los nombres vernaculares siguientes: *brea caspi*, *casharana*, y *sacha parinari*. Es usado como madera redonda en la construcción de viviendas, llegándose a comercializar bajo esta modalidad.

Muestras examinadas. Peru. loreto: Provincia de Maynas, Río Momon, *Croat 19885* (M, MO, AMAZ); misma localidad, *Rimachi 3082* (AMAZ); Río Itaya, *Croat 19210* (M, MO, AMAZ); misma localidad, *Revilla 1924* (MO, AMAZ, USM); Río Nanay, *McDaniel 16303* (AMAZ); misma localidad, *Rimachi 1848, 1960, 2335, 3161* (AMAZ); Puerto Almendras, *Vásquez 5517, 7634, 7652, 7659* (MO, AMAZ, USM); Mishana, *Vásquez 5382, 7997* (MO, AMAZ, USM); Moronillo, *Vásquez 5552* (MO, AMAZ, USM); Río Mazán, *Gentry 16655* (MO, AMAZ, USM); Moronacocha, *Arévalo 62* (AMAZ).

Caraipa grandifolia subsp. *grandifolia* Mart.

Látex transparente oleoso en el fuste, y blancuzco en las ramitas. Hojas dísticas, subcoriáceas, envéz con pelos estrellados sésiles, las hojas jovenes con pelos estrellados pedunculados y con buliformes células epidérmicas protuberantes. Cápsula tomentosa, trígona-piramiforme, simétrica o ligeramente curvada en el ápice. Habita suelos húmedos con mal drenaje llamados localmente: *aguajales* o *sacha aguajales*, muchas veces sometidos a los extremos de las inundaciones estacionales. Frutifica de diciembre hasta abril. A ésta especie se conoce localmente con el nombre vernacular *aceite caspi*. Se usa como madera redonda en la construcción de viviendas rurales.

Muestras examinadas. Peru. loreto: Provincia de Maynas, Mishana, *Gentry 28947* (MO, AMAZ, USM); Puerto Almendras, *Vásquez 6211* (MO, AMAZ, USM); Provincia de Ramón Castilla, Quebrada Ponaico, *Vásquez 7332* (MO, AMAZ).

Caraipa myrcioides Ducke

Hojas dísticas, subcoriáceas, glabras, envéz liso, sin células epidérmicas protuberantes. Habita suelos aluviales inundables.

Muestras examinadas. Peru. madre de dios: Provincia de Tambopata, Cocha cashu, *Gentry 26911, 43447* (MO, AMAZ, USM); pasco: Provincia de Oxapampa, Cabeza de mono, *Gentry 41648, 41727* (MO, AMAZ, USM).

Caraipa punctulata Ducke

Látex amarillo, ± fluido. Hojas dísticas, cartáceas o subcoriáceas, envéz con pelos estrellados sésiles y con buliformes células epidérmicas protuberantes. Cápsula glabra o escazamente cubierta con diminutos pelos estrellados dispersos, trígona-piramiforme, simétrica o ligeramente curvada en el ápice. Habita suelos con mal drenaje, localmente llamados *aguajales* o *sacha aguajales*, preferentemente en la transición entre éstos y el bosque no inundable por embalse, como también las pendientes de los riachuelos. Florece en octubre, y frutifica en enero. A esta especie se conoce con el nombre vernacular *azufre caspi*.

Muestras examinadas. Peru. loreto: Provincia de Requena, carretera en construcción Requena a Jenaro Herrera, *Vásquez 4816* (MO, AMAZ, USM); Provincia de Maynas, Allpahuayo, *Vásquez 5751, 6184* (MO, AMAZ, USM).

Caraipa tereticaulis Tul.

Látex amarillento viscoso, oxidando a blanco y solidificándose al contacto con el aire. Hojas dísticas, subcoriáceas a coriáceas, envéz con diminutos pelos estrellados sésiles dispersos, y buliformes células epidérmicas protuberantes. Cápsula glabra o con diminutos pelos estrellados dispersos, trígona-piramiforme simétrica o ligeramente curvada. Habita preferentemente suelos de arena blanca, muchas veces de extrema infertilidad, comportándose como gregaria con individuos de reducido diámetro, formando bosque enano de 4–5 m de alto, llamado localmente *chamizal*. Florece en agosto, y frutifica en enero. A ésta especie se conoce localmente con los nombres vernaculares siguientes: *aceite caspi blanco*, *brea caspi del varillal*, y *boa caspi*. Se usa como madera redonda para la construcción de viviendas llegándose a comercializar bajo esta modalidad.

Muestras examinadas. PERU. LORETO: Provincia de Maynas: Puerto Almendras, *Vásquez 5519, 5520* (MO, AMAZ, USM); Mishana, *Vásquez 6143, 7952* (MO, AMAZ, USM); misma localidad, *Gentry 24978* (MO, AMAZ, USM); Provincia de Requena, Jenaro Herrera, *Vásquez 7661* (MO, AMAZ, USM); misma localidad, *Freitas 03, p2 LVII* (AMAZ).

Caraipa valioi Paula

Es la especie peruana de *Caraipa* con árboles más grandes siendo su altura regular cerca de los 30 m y diámetro de 70 cm. Tiene látex oleoso, viscoso, y un poco más transparente que las otras especies. Hojas son dísticas, coriáceas a subcoriaceas, con envéz lizo, sin células epidérmicas protuberantes. Cápsulas tomentosas, trigonas-oblicuas o trígonas-subglobosas, asimétricas. Habita suelos arcillosos arenosos, frecuentemente en zonas pantanosas o en los nacimientos de las quebradas. Florece en septiembre. A esta especie se conoce con el nombre vernacular *aceite caspi*. Se usa como madera redonda en la construcción de viviendas, y también en aserrío.

Muestras examinadas. PERU. LORETO: Provincia de Maynas, Puerto Almendras, *Vásquez 6309* (MO, AMAZ, USM); Río Tahuayo, *Vásquez 6754* (MO, AMAZ, USM); Provincia de Requena, Jenaro Herrera, *Vásquez 9618* (MO, AMAZ, USM).

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PHYLOGENETIC ASSESSMENT AND REVISED CIRCUMSCRIPTION OF *CISTANTHE* SPACH (PORTULACACEAE)[1]

Mark A. Hershkovitz[2]

ABSTRACT

Reexamination of Carolin's cladistic analysis of Portulacaceae confirms that *Cistanthe* Spach should be segregated from *Calandrinia* Kunth and should include *Philippiamra* Kuntze. *Calyptridium* Nutt. in Torrey & A. Gray (including *Spraguea* Torrey) cannot be excluded from *Cistanthe* on phylogenetic grounds and is therefore recognized as a section therein. In all, *Cistanthe* includes 45–50 western American species in five sections, including *Cistanthe* sect. *Cistanthe*, *C.* sect. *Amarantoideae* (Reiche) Carolin ex Hershkovitz, *C. Calyptridium* (Nutt. in Torrey & A. Gray) Hershkovitz, *C.* sect. *Philippiamra* (Kuntze) Hershkovitz, and *C.* sect. *Strophiolum* (B. Mathew) Hershkovitz. The phylogenetic relationship of *Cistanthe* to other Portulacaceae indicated in Carolin's cladogram is, upon reanalysis, equivocal, and the relationships among the sections remain poorly understood. Biogeographic understanding of the taxa here included in *Cistanthe* has been obscured by earlier, unnatural, and sometimes erroneous classifications of these plants.

Cistanthe Spach is a putatively monophyletic genus of Portulacaceae comprising five sections and perhaps 45–50 western American species formerly classified in *Calyptridium* Nutt. in Torrey & A. Gray, *Philippiamra* Kuntze (≡ *Silvaea* Philippi), *Spraguea* Torrey, five sections of *Calandrinia* Kunth, and one subgenus of *Lewisia* Pursh (see Table 1 for sectional key, citations, and synonymy). In the present paper, I describe the taxonomic history of *Cistanthe*, evidence for its naturalness as a genus, its relationship to other Portulacaceae, evidence on phylogenetic relationships among the species, and its biogeography.

TAXONOMIC HISTORY

Spach (1836) segregated the Chilean species *Calandrinia grandiflora* Lindley, *C. glauca* Schrader, *C. discolor* Schrader, and *C. speciosa* Lehm. into a new genus, which he named *Cistanthe*. Virtually all subsequent workers (e.g., Franz, 1908; Kelley, 1973; McNeill, 1974; Nyanyano, 1986, 1990; Pax & Hoffmann, 1934; Reiche, 1897, 1898) continued to recognize these species in *Calandrinia* sensu lato (see Carolin, 1987). *Calandrinia* in the broadest sense includes more than 100 species of western North America, western South America, and Australia (Carolin, 1987, in press; Kelley, 1973).

Reiche (1897, 1898), in a revision of Chilean Portulacaceae, recognized 12 sections of *Calandrinia* s.l., including *Calandrinia* sect. *Cistanthe*, which corresponded to Spach's (1836) generic circumscription of *Cistanthe*. Reiche's (1897, 1898) keys and descriptions make evident a close interrelationship among *Calandrinia* sects. *Andinae*, *Arenariae*, *Cistanthe*, and *Rosulatae* (collectively, *Cistanthe* sect. *Cistanthe*) based on the common presence of distinctive, resinous-appearing, black bract and sepal markings (Carolin, 1987) and often pubescent seeds (Kelley, 1973). Reiche did not propose a common category comprising these four sections, which differ primarily with respect to plant size and branching habit (Carolin,

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TABLE 1. Taxonomy of *Cistanthe* Spach. Provided below is a key to the sections of *Cistanthe*, along with full citations, synonymy, and distributions (see Hershkovitz, 1990a).

1a. Stigmas and capsule valves 3(–4); sepals herbaceous, marked or unmarked; petals usually 5 or more; seeds strophiolate or estrophiolate, pubescent or glabrous.
2a. Sepals herbaceous, marked or unmarked; pedicels mostly ≥ 2 mm; seeds strophiolate, pubescent or glabrous; sinuous and ribbonlike veins present or absent; western North America and western South America.
3a. Sepals marked with black etchings; petals 5(–8); seeds mostly pubescent; plants perennial or annual, rarely without cauline leaves; sinuous and ribbonlike veins rarely absent; western South America and southwestern North America. ..... *Cistanthe* sect. *Cistanthe*
3b. Sepals unmarked; petals (7–)8–9(–12); seeds glabrous; plants perennial with basal leaves only; sinuous and ribbonlike veins absent; Washington and British Columbia. ..... *Cistanthe* sect. *Strophiolum*
2b. Sepals membranous, unmarked; pedicels mostly ≤ 2 mm; seeds estrophiolate, glabrous; sinuous and ribbonlike veins present; western South America. ..... *Cistanthe* sect. *Amarantoideae*
1b. Stigmas 2 and capsule valves 2 or none; sepals usually membranous at least along margin, unmarked; petals 4 or fewer; seeds estrophiolate, glabrous.
4a. Fruit dehiscent by two valves; sepals rarely nearly completely herbaceous; ovules mostly more than 1; North America. ..... *Cistanthe* sect. *Calyptridium*
4b. Fruit indehiscent or irregularly dehiscent; sepals membranous; ovule 1; South America. ..... *Cistanthe* sect. *Philippiamra*

Cistanthe Spach, Hist. Nat. Vég. 5: 229. 1836.

1. *Cistanthe* sect. *Cistanthe*. LECTOTYPE: *Calandrinia grandiflora* Lindley.
Calandrinia sect. *Cistanthe* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897.
Calandrinia sect. *Arenariae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.
Calandrinia sect. *Andinae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.
Calandrinia sect. *Rosulatae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.
Ca. 30 spp. from Chile, Argentina, and Peru; 2 spp. from California/Mexico.
2. *Cistanthe* sect. *Strophiolum* (B. Mathew) Hershkovitz, Phytologia 68: 268. 1990. *Lewisia* subg. *Strophiolum* B. Mathew, The Genus *Lewisia* 139. 1989. LECTOTYPE: *Calandrinia tweedyi* A. Gray
1 sp. from Washington and British Columbia.
3. *Cistanthe* sect. *Amarantoideae* (Reiche) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. *Calandrinia* sect. *Amarantoideae* Reiche, Ber. Deutsch. Bot. Ges. 15: 501. 1897. LECTOTYPE: *Calandrinia salsoloides* Barnéoud in Gay.
Ca. 4 spp. from Chile, Argentina, and Peru; 1 sp. from California, Arizona, and Mexico.
4. *Cistanthe* sect. *Calyptridium* (Nutt. in Torrey & A. Gray) Hershkovitz, Phytologia 68: 267. 1990. *Calyptridium* Nutt. in Torrey & A. Gray, Fl. N. Amer. 1(2): 198. 1838. TYPE: *Calyptridium monandrum* Nutt. in Torrey & A. Gray.
Spraguea Torrey, Pl. Frémont. Smithsonian Contr. Knowl. 6(2) [err., 5(1)]: 4. 1853.
Ca. 8 spp. from western North America.
5. *Cistanthe* sect. *Philippiamra* (Kuntze) Hershkovitz, Phytologia 68: 269. 1990. *Philippiamra* Kuntze, Revis. Gen. Pl. 1: 58. 1891. LECTOTYPE: *Silvaea celosioides* Philippi.
Silvaea Philippi, Fl. Atacam. 22. 1860 (non *Silvaea* J. D. Hook. & Arn. ex Baillon, 1858).
2–4 spp. from Chile and Peru.

1987; Reiche, 1897, 1898). Reiche (1897) noted the similarity between *Cistanthe* sects. *Amarantoideae* and *Philippiamra*, but he classified the former in *Calandrinia* sect. *Amarantoideae* and the latter in *Silvaea* (see Table 1).

Pax & Hoffmann (1934), in their taxonomic revision of Portulacaceae, classified *Cistanthe* sects. *Amarantoideae* and *Cistanthe* (as part of *Calandrinia* s.l.) in Calandrinieae–Calandriniinae; *Cistanthe* sect. *Calyptridium* (as *Calyptridium* and *Spraguea*), in Calandrinieae–Calyptridiinae; and *Cistanthe* sect. *Philippiamra* (as *Philippiamra*) in an informal group described as intermediate between Portulacaceae and Basellaceae. The sections of *Cistanthe*, in their former generic assignments, were each taxonomically associated with other relatively distantly related members of Portulacaceae (Carolin, 1987). Thus, Caladriniinae also included *Talinum* Adans., *Anacampseros* L., and other genera; Calyptridiinae included *Monocosmia* Fenzl [= *Calandrinia* sect. *Monocosmia* (Fenzl) Hershkovitz (Hershkovitz, 1990b, 1991b, in press a)]; and *Philippiamra* was associated with *Ceraria* Pearson & Stephens and *Portulacaria* Jacq. (Carolin, 1987; Pax & Hoffmann, 1934). As noted above, *Cistanthe* sect. *Strophiolum* was thought to belong in *Lewisia*, which Pax & Hoffmann placed in tribe Portulaceae along with *Portulaca* L.

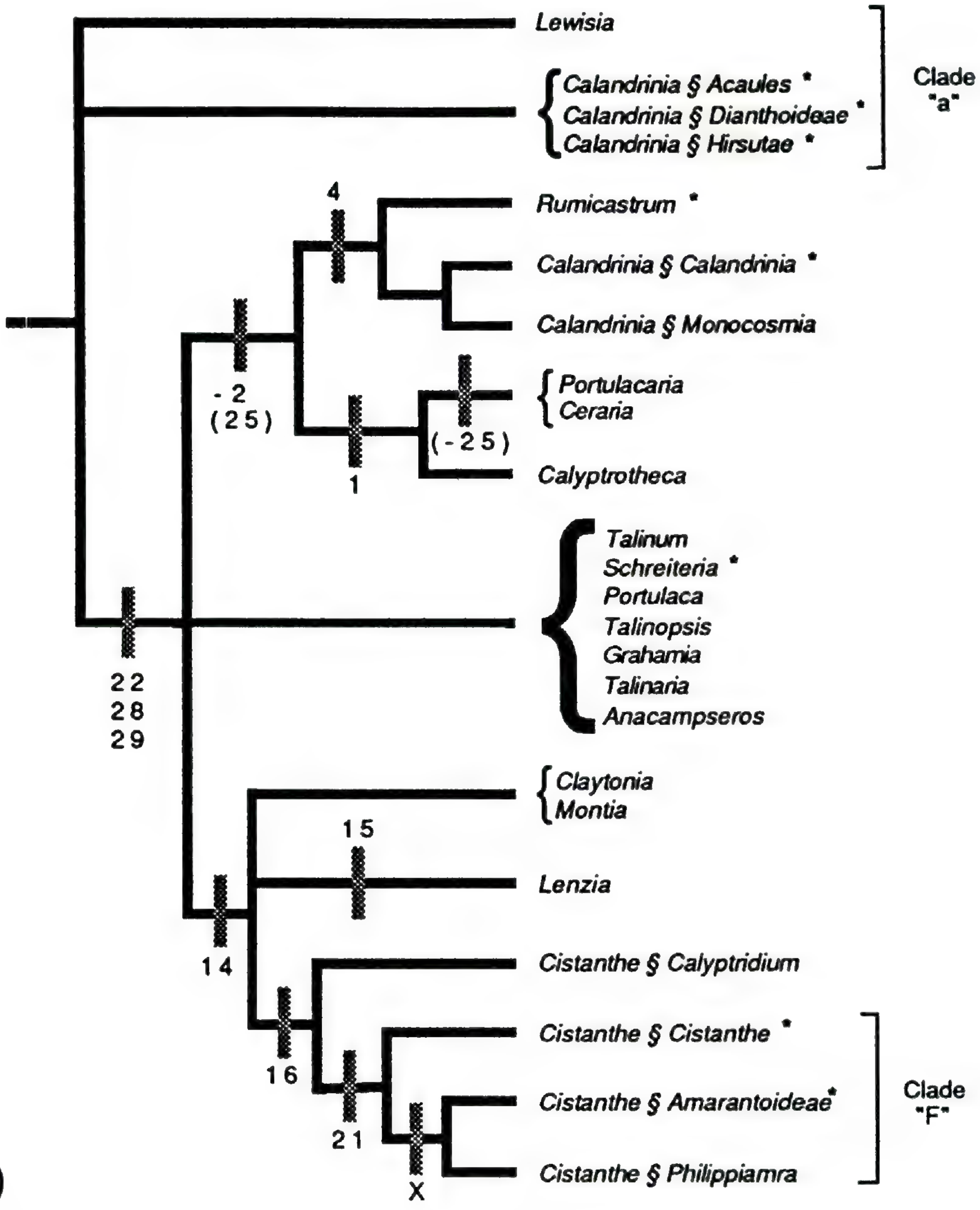

FIGURE 1. Simplified reproduction of Carolin's (1987: 402, fig. 7) most parsimonious cladogram of Portulacaceae, emphasizing the relationships among major clades and among members of *Cistanthe*. Taxa comprising traditional *Calandrinia* are starred. Only character state changes relevant to the present discussion of *Cistanthe* are shown. The numbered characters and "X" are Carolin's (see Table 2). All of the character state changes shown are regarded here as problematic (see text).

Kelley (1973), in his survey of seed and trichome morphology in the genus, maintained that *Calandrinia* s.l. was a natural assemblage. The traits Kelley cited as common to all the species (two sepals, three carpels, free-central placentation) are, cladistically, symplesiomorphic with many to all Portulacaceae. Kelley recognized the close interrelationship between *Calandrinia* sects. *Andinae*, *Arenariae*, *Cistanthe*, and *Rosulatae* (i.e., among members of *Cistanthe* sect. *Cistanthe*). Like Reiche (1897), Kelley remarked on the morphological similarities between *Cistanthe* sects. *Amarantoideae* and *Philippiamra*, but he did not recommend including these in a common genus.

McNeill's (1974) tribal classification of Portulacaceae is similar to that of Pax & Hoffmann (1934) in that the components of *Cistanthe* are placed in four different tribes.

Nyanyano (1986), in a revision of Portulacaceae, divided *Calandrinia* s.l. into three sections, but the sectional circumscriptions are anomalous and accord neither with those proposed elsewhere (cf. Carolin, 1987, in press; Kelley, 1973; Reiche, 1897, 1898), nor with the characterizations in his sectional key. Furthermore, many species of *Calandrinia* s.l., including all of the Australian element, are not accounted for in his treatment. In Nyanyano's three-section classification of *Calan-*

drinia s.l., members of *Cistanthe* sect. *Cistanthe* are included in two of the sections, while *Cistanthe* sect. *Amarantoideae* is included in the third. Each of Nyanyano's three sections includes taxa that, according to Carolin (1987) and Hershkovitz (1990b, in press a), belong in different genera. Although Nyanyano (1986, 1990) recognized the relationship between *Cistanthe* sects. *Calyptridium* and *Philippiamra* (as distinct genera) and included both in tribe Calyptridieae, his circumscription of Calyptridieae is otherwise unnatural, and he went so far as to include *Monocosmia* in *Calyptridium* (cf. Hershkovitz, in press a).

Carolin (1987), in his phylogenetic analysis of Portulacaceae, divided the existing sections of *Calandrinia* s.l. (see Cullen, 1953; von Poellnitz, 1934; Reiche, 1897, 1898) into 11 OTUs (excluding *Calandrinia* sect. *Partitae* von Poellnitz, which belongs in *Anacampseros*; see Carolin, 1987; Kelley, 1973). Carolin's OTU *Cistanthe* comprised *Calandrinia* sects. *Andinae*, *Arenariae*, *Cistanthe*, and *Rosulatae*. Perhaps the most significant finding of Carolin's analysis was that the OTUs of *Calandrinia* s.l. showed cladistic relationships with various genera throughout Portulacaceae, indicating that its erstwhile circumscriptions were unnatural (Fig. 1). The OTU *Cistanthe*, along with the OTUs *Amarantoideae* (= *Cistanthe* sect. *Amarantoideae*) and *Silvaea* (= *Cistanthe* sect. *Philippiamra*), formed clade "F" in Carolin's (1987, fig. 7) cladogram. Although lacking an unequivocal synapomorphy (see below), clade "F" corresponded with Carolin's (1987, in press) proposed generic circumscription of *Cistanthe*. Carolin (in press) proposed combining the OTUs *Amarantoideae* and *Silvaea* in a single section named for the former. In Carolin's (1987) analysis, clade "F" formed the sister group to the OTU *Calyptridium* (= *Cistanthe* sect. *Calyptridium*). Clade ["F" + *Calyptridium*] was diagnosed by one unique and nearly universally shared feature: the presence of unequal bracts associated with the inflorescence nodes (Fig. 2). Carolin (1987, in press) maintained *Calyptridium* as a distinct genus, however.

The present paper basically follows Carolin's (1987, in press) recommendation that *Cistanthe* be segregated from *Calandrinia* s.l., but the circumscription is modified to include *Calyptridium* and *Lewisia* subg. *Strophiolum* as distinct sections, and Carolin's OTUs *Amarantoideae* and *Silvaea* are each assigned to their own section (see Table 1).

Phylogenetic Assessment of *Cistanthe*

Figures 1 and 3 depict the relationships among Portulacaceae as determined in Carolin's (1987, fig. 7) cladistic analysis and subjectively reanalyzed here. As discussed below, these figures emphasize evidence pertaining to the monophyly of *Cistanthe*, the relationship of the genus to other Portulacaceae, and relationships within the genus. The taxonomy in Figures 1 and 3 follows Carolin (1987, in press), except for *Cistanthe* and *Calandrinia*, which follows Hershkovitz (1990a, b, 1991b, in press a). The numbered characters are defined in Table 2. Figure 1 depicts Carolin's consensus tree and shows the character state changes occurring between the root of the tree and the terminal OTUs of *Cistanthe*, as well as selected character state changes that are relevant to the present discussion but involve other branches of the tree. All of the indicated synapomorphies are regarded here as equivocal or unwarranted, as explained below. Figure 3 emphasizes possible phylogenetic relationships among the sections of *Cistanthe* as speculated here on the basis of the data in Table 3 and shows the relationships of *Calandrinia* sects. *Calandrinia* and *Monocosmia* I have proposed elsewhere (Hershkovitz, 1990b, in press a). *Cistanthe* sect. *Strophiolum* is not shown in Figure 1 because Carolin was unaware of the relationship of this taxon to *Cistanthe* rather than *Lewisia* (Hershkovitz, 1990b, in press b).

1. The monophyly of *Cistanthe*

Although the monophyly of *Cistanthe* in the circumscription proposed here is evidenced by only a single synapomorphy (Figs. 1, 3), additional traits reinforce the close interrelationships between the sections. For example, leaves of *Cistanthe* generally have winged (if present) petioles, clasping leaf bases, festooned brochidodromous venation (if sufficiently broad to show this trait), a primary vein that becomes obsolete at the leaf apex, ribbonlike veins, sinuous veins, and predominantly brachyparacytic stomata (Hershkovitz, 1990b, in press b, 1991c). The combination of these leaf traits is absent among other Portulacaceae, although their value in cladistically diagnosing the genus remains uncertain.

2. Phylogenetic relationship of *Cistanthe* to other Portulacaceae

Subjective reanalysis of Carolin's (1987) data in light of additional evidence from leaf morpho-

logical studies (Hershkovitz, 1990b, in press b, in press c, in prep.) indicates that the western American members of Portulacaceae (Fig. 3; Carolin, 1987, fig. 8; Hershkovitz, 1990b, 1991a, c, in prep.), including *Cistanthe*, form a cohesive and possibly monophyletic group. The western American taxa share similar habit, leaf base, petiole, and stomatal morphology (Hershkovitz, 1991a, in prep.). The distinction between the western American group and the eastern American/African group of Portulacaceae with respect to these characters suggests that one or more of the characters may help cladistically diagnose either group. The Australian endemic *Rumicastrum* Ulbrich (cf. Fig. 3), however, is morphologically intermediate between these two groups (Hershkovitz, 1990b, in press a, in prep.). The precise relationships of *Cistanthe* to other western American taxa remain uncertain pending additional analysis.

The phylogenetic relationships of *Cistanthe* indicated in Carolin's cladogram (Fig. 1) are more equivocal than they appear to be. The synapomorphies that diagnose Portulacaceae (including *Cistanthe*) minus Carolin's "secondary" clade "a" (not a clade in Carolin's consensus tree, Fig. 1) are problematic for several reasons. The synapomorphies are the change from more than five to five or fewer petals (character 22), and the two-step change from five or more to four to three or fewer stigmas (characters 28 and 29). Five petals and/or three stigmas characterize several species in each of the excluded OTUs, however (see Mathew, 1989, for *Leuisia*; and Reiche, 1898, for the pertinent sections of *Calandrinia*), and these characters show considerable reversal and rederivation in the clade diagnosed by low petal and stigma numbers (Carolin, 1987). The variability of these characters within and among the OTUs renders highly critical the accuracy of the character polarity assessment. Carolin based his polarity assessments for these characters in Portulacaceae (and, presumably, his assumptions on primitive states within OTUs) on the outgroup relationships proposed in Rodman et al.'s (1984) cladistic analysis of Centrospermae. In fact, based on that study, the polarities of these characters would be equivocal because one outgroup (Aizoaceae + Cactaceae) was scored for having high petal and stigma numbers, whereas the other (Basellaceae + Didieriaceae) has low petal and stigma numbers exclusively. This point is moot, however, because Rodman et al.'s (1984) character definitions and/or scores for floral characters and, for that matter, most aspects of their phylogenetic analysis have been heavily criticized (Levin, 1985; Bittrich, 1990; Bittrich & Hartmann, 1988; Hershkovitz, 1989; Rodman, 1990). Also, I have elsewhere (Hershkovitz, 1991a, in prep.) maintained that Cactaceae, Didieriaceae, and Basellaceae are each phylogenetically nested among Portulacaceae.

Carolin's (1987) treatment of the petal and stigma characters is problematic for other reasons as well. For example, it is not clear whether petals in Portulacaceae are homologous to the sepals or stamens of apetalous Centrospermae, to similar structures in other "petaloid" Centrospermae, or even to petals in the currently unknown outgroups of Centrospermae (see Cronquist, 1981, 1988; Levin, 1985; Rodman, 1985). Also, the change from five to three stigmas should not require two steps, as it does in Carolin's (1987) analysis.

In the absence of unequivocal outgroup rela-

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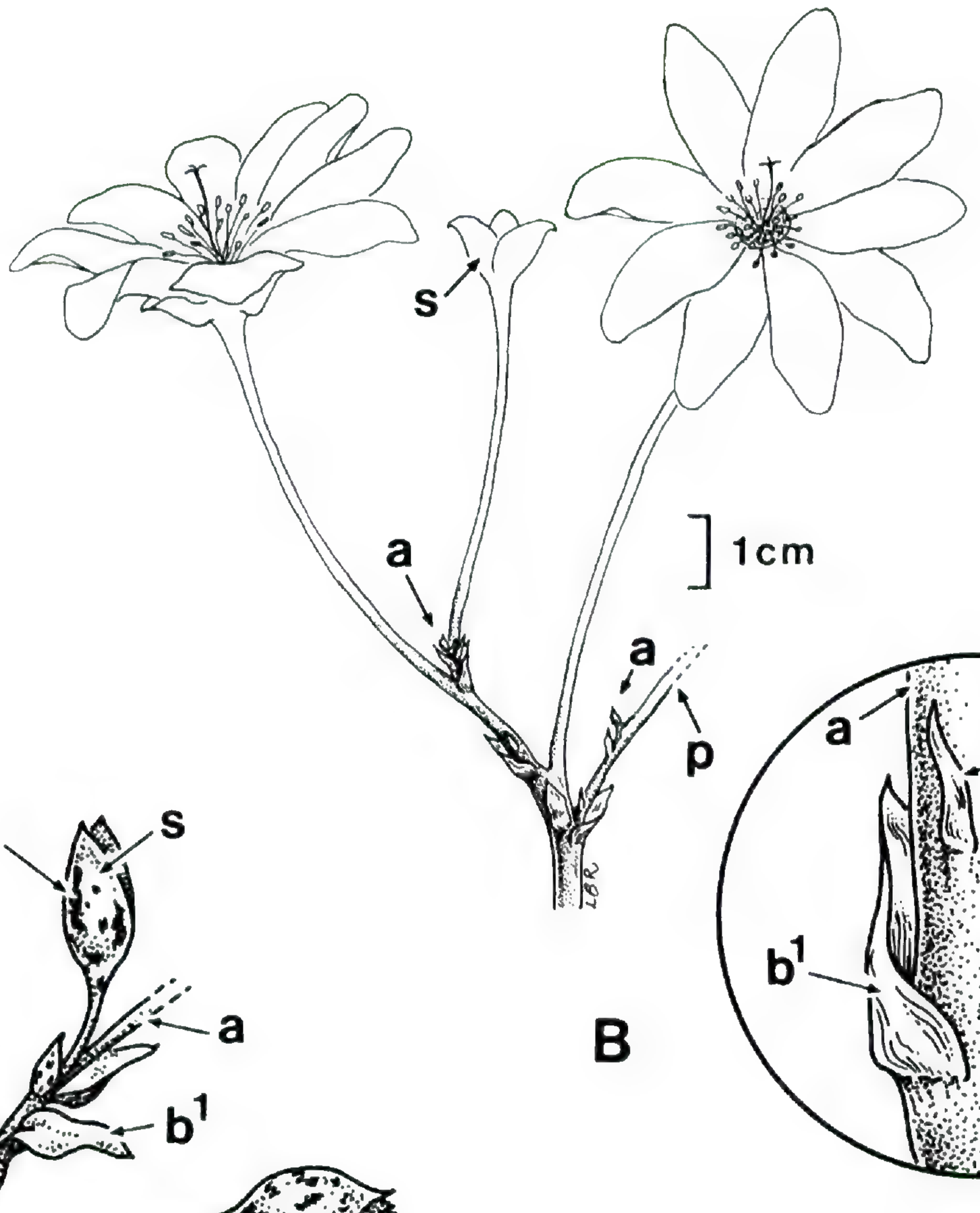
FIGURE 2. Inflorescence bract morphology in *Cistanthe*.—A. *C.* (*Cistanthe*) *grandiflora* (*Ford & Penalosa 497*, MO). Terminal portion of inflorescence showing unequal bracts at the flowering nodes and bract and sepal markings.—B. *C.* (*Strophiolum*) *tweedyi* (*Thompson 6463*, US). Portion of inflorescence showing (inset) unequal bracts at the flowering node. The smaller bract is displaced apically on the continuing axis. (Modified from Hershkovitz, in press b.)—C. *C.* (*Amarantoideae*) *calycina* (*Johnston 5313*, US). Terminal portion of inflorescence showing (inset, with all but the uppermost flowers absent) unequal bracts associated with the flowering nodes.—D. *C.* (*Philippiamra*) *celosioides* (*Zollner 7811*, NA). Terminal portion of inflorescence showing (inset, with the upper two flowers absent) unequal bracts at the flowering nodes.—E. *C.* (*Calyptridium*) *parryi* var. *parryi* (*Munz 5726*, UC). Terminal portion of inflorescence showing (inset, with upper and lower flowers absent) unequal bracts associated with the flowering nodes. The smaller of the two associated inflorescence bracts is usually adjacent to the pedicel, while the larger bract occurs a short distance below.—F. *C.* (*Calyptridium*) *monosperma* (*Johannsen 2394*, UC). Terminal portion of inflorescence showing (inset, with all but the uppermost flower absent) single large bract associated with the swollen flowering nodes. The flowers are arranged in a two-ranked alternating pattern on the convex side of the coiled inflorescence branches, and the bracts are likewise arranged on the concave side. The inflorescence nodes are swollen, and the pedicels are inserted in shallow sockets. a, continuing axis; b, bract; b^1, larger of the pair of bracts associated with the node; b^2, smaller of the pair of bracts associated with the node; m, black bract/sepal markings; p, pedicel; s, sepal; x, scar from removed or abscised flower. (Drawings by Lesley Randall.)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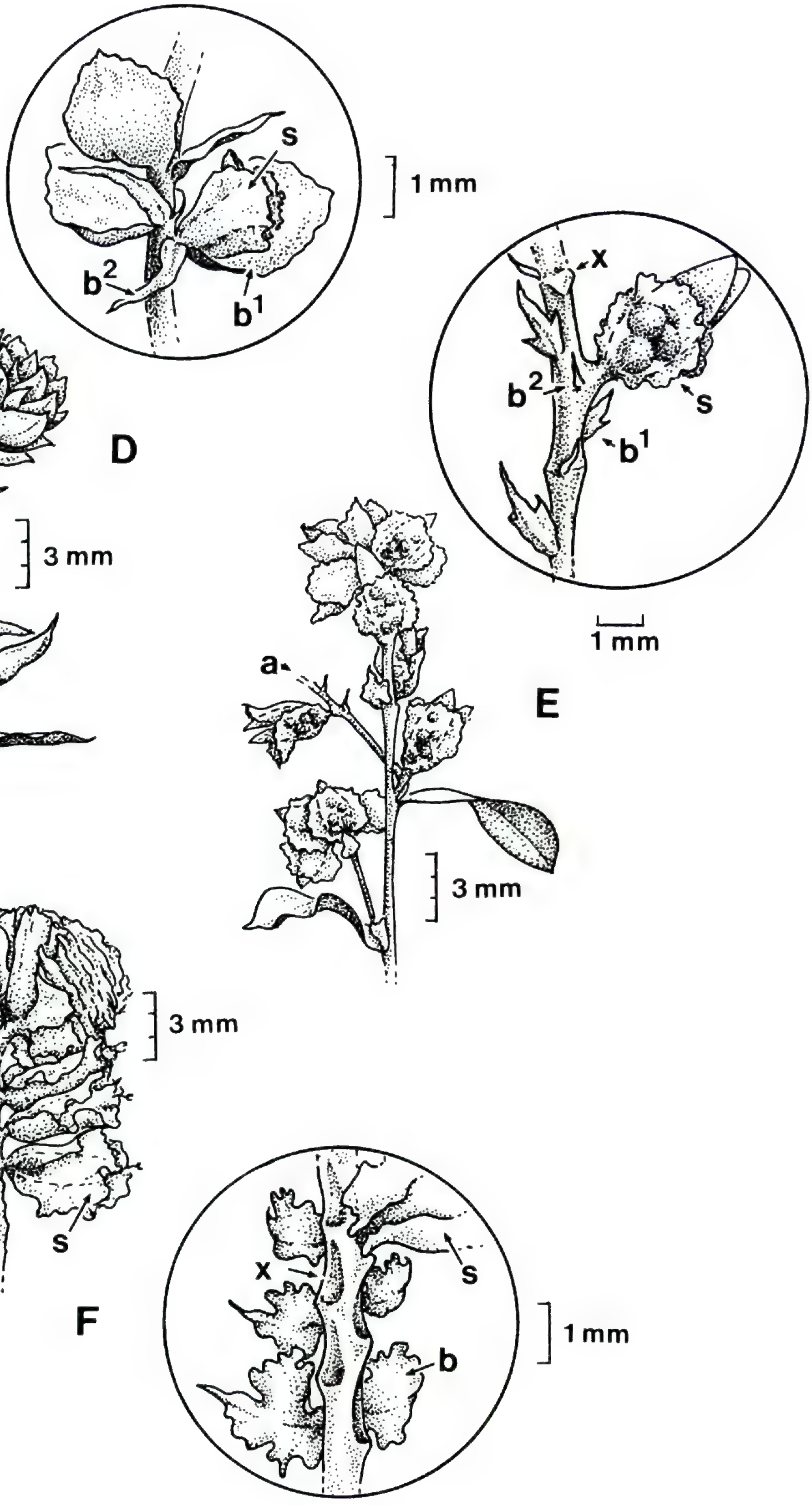
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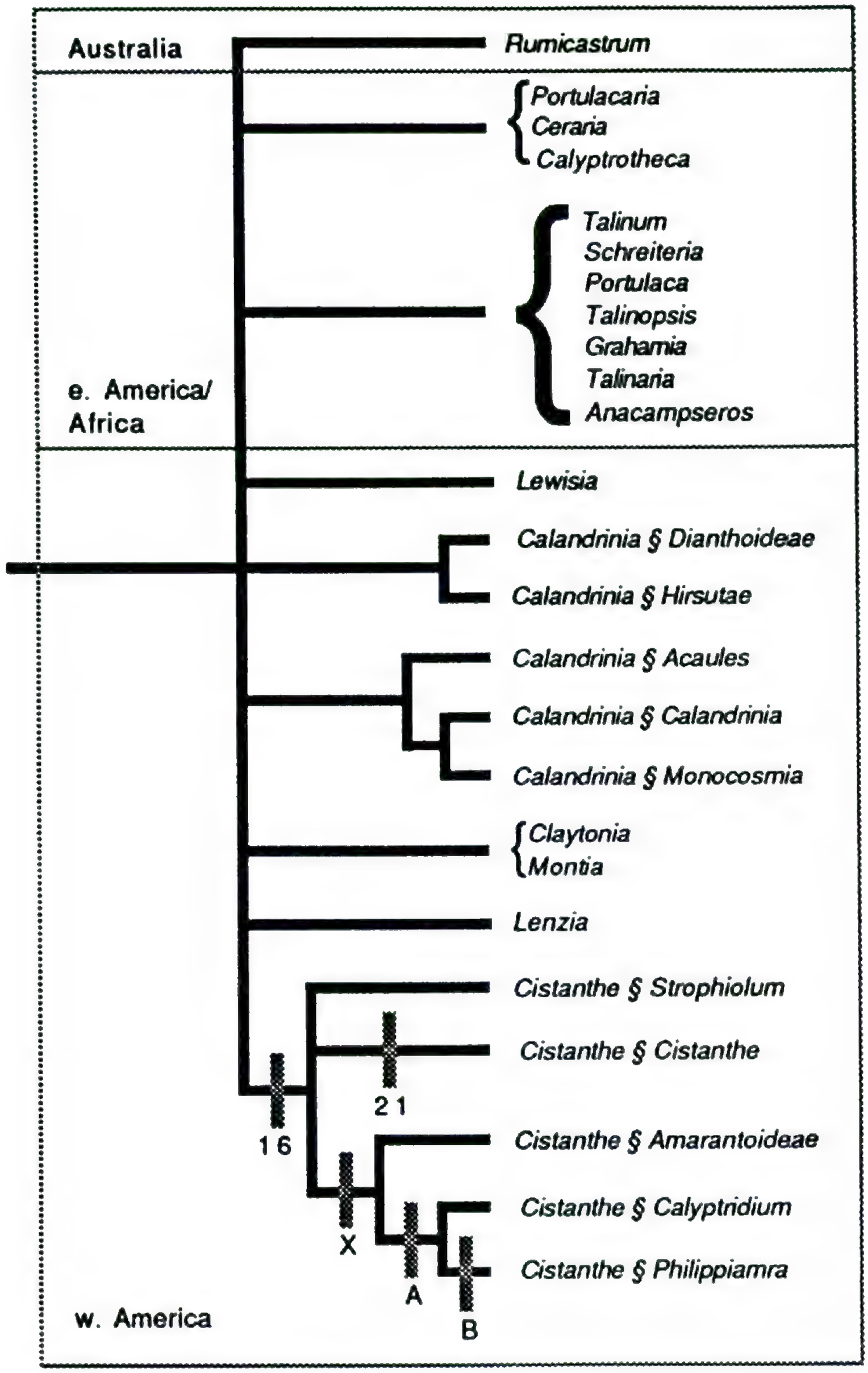

FIGURE 3. Revised cladogram of Portulacaceae derived by eliminating the questionable synapomorphies indicated in Figure 1 (see text). The numbered and lettered characters are defined in Table 2. The relationships shown for *Calandrinia* sects. *Calandrinia* and *Monocosmia* are after Hershkovitz (1990b, in press a), and the relationships shown among the members of *Cistanthe* are discussed in the present text. The boxes enclosing portions of the diagram circumscribe the regions of endemism or greatest endemism of the included taxa (Carolin, 1987; Hershkovitz, in press a, in prep.).

tionships for Portulacaceae, the evolutionary polarity of petal and stigma numbers for this family cannot be determined a priori, nor can primitive states be arbitrarily designated in those genera variable for these characters. In the context of Carolin's cladogram, therefore, the synapomorphies diagnosing the basal node must be regarded as unwarranted.

Because the basis for the exclusion of Carolin's (1987) clade "a" from the remainder of Portulacaceae (Fig. 1) is questionable, the sole synapomorphy that diagnoses the clade (*Lenzia* Philippi + *Cistanthe* (in the present sense) + tribe Montieae Dumort.), the derivation of a monochasial inflorescence from "dichasia passing into monochasia" (character 14), also becomes problematic. Monochasia and/or solitary flowers occur in several members of clade "a." Dichasial inflorescence

TABLE 2. Characters referred to in Figures 1 and 3. The numbered characters and character "X" correspond to Carolin's (1987: 392, 412, appendix 3). The character states given first are those supposed by Carolin to be primitive. The polarities for characters 1, 2, and 4 are derived from Carolin's text because those indicated in his appendix appear erroneous. Some of Carolin's polarity determinations are discussed in the present text. Characters A and B are defined here; the state given first is considered primitive.

Character no.	Character: primitive state vs. derived state
1	Growth form: not phanerophyte vs. phanerophyte
2	Growth form: not suffruticose and/or passive chamaephyte vs. suffruticose and/or passive chamaephyte
4	Growth form: not therophyte vs. therophyte
14	Inflorescence: "dichasial passing into monochasia" vs. monochasial or solitary
15	Inflorescence: not solitary vs. solitary
16	Inflorescence bracts: equal vs. unequal
21	Sepal markings: absent vs. present
22	Petals: more than 5 vs. 5 or less
25	Pollen: trizonocolpate vs. panporate
28	Stigmas: 5 or more vs. less than 5
29	Stigmas: 4 or more vs. less than 4
31	Fruit: dehiscent vs. indehiscent
X	Inflorescence: open with long pedicels vs. condensed with short pedicels
A	Carpel number: 3 or more vs. 2
B	Fruit: indurate vs. membranous

branching in *Lewisia* is restricted to species of *L.* sect. *Cotyledon* J. E. Hohn ex B. Mathew, and there is no strong evidence that section is otherwise primitive within the genus (Hershkovitz, 1990b, in press b; but see also Hohn, 1975); i.e., the dichasia might be secondarily derived. Reiche (1897) and Hershkovitz (1990b) reported that dichasial branching rarely occurs in *Cistanthe*, but this is questionable (Hershkovitz, in press b). Closer examination of herbarium specimens reveals that superficially dichasial branching results when the internodes are not elongated.

The scoring of inflorescence types in Carolin's (1987) analysis is problematic for other reasons as well. Because the primitive state could not be assessed by outgroup comparison, Carolin based his inflorescence character transformation series on "general principles," presuming that metaxytriads are primitive among Portulacaceae. I suspect that Carolin is correct in this regard; nevertheless, in his cladogram, the taxa scored for having metaxy-

TABLE 3. Character states in the sections of *Cistanthe*. The sections of *Cistanthe* are listed in the first row. The outgroups are inferred to be the remainder of Portulacaceae; the likely primitive character states, where known, are indicated. Parentheses denote rare character states.

Character	Outgroups	*Strophiolum*	*Cistanthe*	*Philippiamra*	*Amarantoideae*	*Calyptridium*
Inflorescence	open?	open	open (condensed)	condensed	condensed	condensed
Pedicel length (in flower)	> 2 mm?	> 2 mm	> 2 mm	< 2 mm	usually < 2 mm	usually < 2 mm
Bract/sepal markings	absent	absent	present	absent	absent	absent
Sepal texture (in flower)	herbaceous?	herbaceous	herbaceous	membranous	membranous	mostly membranous, at least along margin
Petal number	?	(7–)8–9(–12)	5(–8)	2–4	5	2–4
Carpel number	≥ 3	3	3(–4)	2	3	2
Capsule dehiscence	valvate	valvate	valvate	indehiscent	valvate	indehiscent
Capsule texture	indurate	indurate	indurate	membranous	indurate	indurate-membranous
Seed pubescence	absent	absent	present/absent	absent	absent	absent
Strophiole	?	present	present	absent	absent	absent
All basal leaves	?	yes	yes/no	no	no	yes/no
Sinuous leaf veins	?	no	yes (no)	yes	yes	yes (no)
Ribbonlike leaf veins	?	no	yes (no)	yes	yes	yes (no)

triads (*Portulacaria*, *Ceraria*, *Calyptrotheca* Gilg, *Portulaca*) are nested among taxa having the supposedly more derived inflorescence types (see Carolin, 1987, fig. 7). Also, Carolin's transformation series requires that solitary flowers be derived from dichasia via monochasia; i.e., in two steps rather than one. This requirement appears to have influenced both the topology and number of steps in the most parsimonious cladogram. For example, except for the assumption that solitary flowers are derived from monochasia, *Lenzia* would not be included in the clade with *Cistanthe* and Montieae (see Fig. 1).

Other problems in Carolin's (1987) cladogram have an indirect effect on the assessment of the position of *Cistanthe* among Portulacaceae. For example, both synapomorphies (Fig. 1, characters 2, 25) supporting the clade comprised of *Rumicastrum*, *Calandrinia* sect. *Calandrinia* (≡ *Calandrinia* sect. *Compressae* Reiche), *Calandrinia* sect. *Monocosmia*, *Portulacaria*, *Ceraria*, and *Calyptrotheca* are problematic. The shared loss of the chamaephytic growth form (character 2) is essentially redundant with the subsequent derivations of the phanerophytic growth form (character 1) in *Calyptrotheca*, *Ceraria*, and *Portulacaria*, and the therophytic growth form (character 4) in *Rumicastrum* and *Calandrinia*. Carolin treated different growth forms as different characters rather than different states of a single character. The derivation of pantoporate from tricolpate pollen (Fig. 1, character 25), which subsequently reverses in the *Portulacaria* + *Ceraria* clade, is equivocal: two independent derivations of pantoporate pollen would be equally parsimonious. In this case, two independent derivations seem more plausible, however, because there is no evidence elsewhere among angiosperms that tricolpate pollen can be rederived from pantoporate. Also, additional reanalyses of Carolin's (1987) cladogram and corroboration with leaf morphological evidence indicate that *Calandrinia* sects. *Calandrinia* and *Monocosmia* actually belong near *Calandrinia* sect. *Acaules* Reiche, rather than next to the *Rumicastrum* clade (Hershkovitz, 1990b, in press a, in press c).

Pending a thorough reanalysis of phylogenetic relationships among members of Portulacaceae and affiliated families, the position of *Cistanthe* will remain uncertain. If the problematic synapomorphies in Carolin's (1987) cladogram described above are disregarded, however, the basal polytomy shown in Figure 3 results. Figure 3 presumes that, in a formal reanalysis of Portulacaceae, *Cistanthe* would remain monophyletic. Preliminary reanalyses (D. Ford, unpublished; Hershkovitz, unpublished) indicate that this will be the case. Figure 3 is not only highly unresolved, it is inherently inaccurate because of the probable paraphyly of Portulacaceae with respect to Basellaceae, Didieriaceae, Hectorellaceae, and possibly also Cactaceae (Hershkovitz, 1989, 1991a, unpublished). Also, two other members of Portulacaceae, *Talinella* Baillon and *Amphipetalum* Bacigalupo in Spichiger, were not included in Carolin's (1987) analysis and are not shown in Figures 1 and 3.

3. PHYLOGENETIC RELATIONSHIPS WITHIN *CISTANTHE*

The relationships among the sections of *Cistanthe* indicated in Figures 1 and 3 presume that all of the sections of *Cistanthe* are monophyletic. The monophyly of *Cistanthe* sect. *Cistanthe* is evidenced only by the universally shared presence of bract and sepal markings (Fig. 2A), although the trait is apparently lacking in aberrant specimens (Hershkovitz, 1991b). The possibility that this section is paraphyletic, therefore, should not be excluded, especially because this group otherwise shows variation for several of the characters listed in Table 3. *Cistanthe* sect. *Strophiolum* is monotypic, hence monophyletic. *Cistanthe* sect. *Philippiamra* appears to be monophyletic based on its fruit morphology. According to Table 3 and Figures 1 and 3, sects. *Amarantoideae* and *Calyptridium* lack an autapomorphy. A potential autapomorphy for sect. *Calyptridium* is the tetraploid condition found in all members of this section (see Hinton, 1975).

Based on their character states for carpel number, capsule dehiscence, and capsule texture, sects. *Amarantoideae*, *Cistanthe*, and *Strophiolum* appear to represent the primitive element of *Cistanthe* (see Fig. 3). Because the precise outgroup relationships of *Cistanthe* are not known, however, the data in Table 3 cannot corroborate an unequivocal hypothesis of relationship among these three sections. If the outgroups lack arils and have cauline leaves, sinuous and ribbonlike veins, and few petals (e.g., some *Rumicastrum* spp.), then sect. *Amarantoideae* likely represents the basalmost clade in the genus, and sect. *Strophiolum* would arise collaterally with sect. *Cistanthe*. If the outgroups possess the alternative states of these characters (e.g., some *Lewisia* spp.), then sect. *Strophiolum* would likely represent the basalmost taxon (see Hershkovitz, in press b)—a result that would have interesting biogeographic implications (see below). Most of the potential outgroups of *Cistanthe* (see Fig. 3), however, do not possess the

entire suite of traits that could unequivocally show either sect. *Amarantoideae* or sect. *Strophiolum* as the basal taxon in *Cistanthe*.

The difference between Carolin's (1987) and the present interpretation of the position of sect. *Calyptridium* can be accounted for, in part, by a problematic synapomorphy indicated in Carolin's cladogram (Fig. 1). Carolin's cladogram indicates that the absence of black bract and sepal markings (character 21) excludes sect. *Calyptridium* from the remainder of the genus. According to Carolin (1987), this trait is weakly evident in members of sect. *Amarantoideae*, but I have found no such evidence in the specimens I examined (see Hershkovitz, 1991b). (Carolin (in press), in his generic key to Portulacaceae, also reported markings in *Rumicastrum* and *Schreiteria* Carolin—I cannot confirm whether markings exist in these taxa.) Even if the markings occur in sect. *Amarantoideae*, however, their absence must be regarded as the primitive state unless this section is presumed to have arisen from within sect. *Cistanthe*. In any case, Carolin misscored sect. *Philippiamra* for having the markings. With this in mind, it should be clear from Figure 1 that sect. *Calyptridium* cannot be excluded from *Cistanthe* on the basis of this character.

The putatively derived position of sect. *Calyptridium* indicated in Figure 3 is based on its possession of a two-carpellate rather than three-carpellate gynoecium (shared with sect. *Philippiamra*), and a condensed rather than more open inflorescence (character "X" in Figs. 1, 3; not unique to sects. *Amarantoideae* and *Philippiamra*, contra Carolin, 1987). Other possibly significant characters (not indicated in Fig. 3) include fruit texture, sepal texture, and pollen morphology. The fruit texture in sect. *Calyptridium* is intermediate between the more indurate of sects. *Amarantoideae*, *Cistanthe*, and *Strophiolum*, and the more membranous of sect. *Philippiamra*. Like sects. *Amarantoideae* and *Philippiamra*, the sepals in sect. *Calyptridium* are usually at least partially membranous (Munz & Keck, 1973) rather than herbaceous (i.e., chlorophyllous). The last character is difficult to evaluate from herbarium specimens—even herbaceous bracts probably become more membranous with age and more so with herbarium processing. Finally, Nilsson (1967) noted a similarity in pollen morphology between sect. *Calyptridium* and sect. *Philippiamra*, although he did not extensively survey other members of *Cistanthe*.

In order to resolve phylogenetic relationships further among the sections of *Cistanthe*, it will be necessary to resolve interspecific relationships within the sections. Only limited inferences can be made at present. For example, three species of sect. *Calyptridium* (*C. umbellata* (Torrey) Hershkovitz, *C. monosperma* (E. Greene) Hershkovitz, and *C. pulchella* (Eastwood) Hershkovitz) that collectively constituted *Spraguea* (Hinton, 1975) lack the smaller of the two bracts that characterize all other *Cistanthe* (Fig. 1E). The close relationship of these three species to the remainder of sect. *Calyptridium* seems beyond doubt (Hinton, 1975), so it seems reasonable to conclude that the former constitute a clade within the latter (and that the controversial genus *Spraguea* does, in fact, represent a natural grouping; cf. Hinton, 1975). *Cistanthe calycina* (Philippi) Carolin ex Hershkovitz and *C. ambigua* (S. Watson) Carolin ex Hershkovitz, both of sect. *Amarantoideae*, have a somewhat more open inflorescence (plesiomorphic?, see Table 3) than other species of the section. *Cistanthe ambigua*, the only North American species of sect. *Amarantoideae*, has especially long pedicels (plesiomorphic?, see Table 3) compared to the other species of this section (Kelley, 1973), but its leaf venation pattern is clearly derived (Hershkovitz, 1990b, 1991c). Thus, the classification of *C. ambigua* in sect. *Amarantoideae* deserves additional scrutiny. *Cistanthe* sect. *Cistanthe* is the most polymorphic and widely distributed section of *Cistanthe*, and while some apparently closely interrelated species groups can be identified (Hershkovitz, 1991b; Kelley, 1973; Reiche, 1898), the overall phylogenetic interrelationships remain obscure. The South American species of sect. *Cistanthe* are especially in need of revision (Hershkovitz, 1991b). Until this is accomplished, attempts to circumscribe taxonomic units for purposes of phylogenetic analysis may be futile. Phylogenetic resolution in sects. *Philippiamra* and *Strophiolum* is trivial. The former is monotypic, and while the number of species in the latter is not well established, the degree of polymorphism is clearly limited (Hershkovitz, 1991b).

Biogeography of *Cistanthe*

Understanding of the biogeography of *Cistanthe* was obscured by pre-Carolin (1987) phylogenetic and biogeographic concepts of Portulacaceae, in which much of *Cistanthe* was included in *Calandrinia* s.l. The latter genus was regarded as basically western South American and Australian (Kelley, 1973; Raven & Axelrod, 1978). The only two North American species of *Cistanthe* formerly included in *Calandrinia* s.l., *C. ambigua* (Mojave

and Sonoran deserts) and *C. maritima* (Nutt. in Torrey & A. Gray) Carolin ex Hershkovitz (coastal California and Baja California), were presumed to have arrived from temperate South America via relatively recent (Quaternary?) long-distance and/or stepwise dispersal (Kelley, 1973; Raven & Axelrod, 1978). *Cistanthe* sect. *Philippiamra* was, presumably, conceived of as disjunct with the South African genera *Ceraria* and *Portulacaria* (see Carolin, 1987). *Cistanthe* sects. *Calyptridium* and *Strophiolum*, as *Calyptridium* and a species of *Lewisia*, respectively, are presumably among those North American Portulacaceae believed to have ultimately had a (temporally and phyletically nonspecific) South American origin (see Raven & Axelrod, 1978).

The present synthesis of *Cistanthe* as illuminated by Carolin (1987) and emended here provides a previously unappreciated example of an amphitropical temperate disjunct taxon having considerable endemism in North and South America. Particularly critical to this biogeographic revelation is the determination that sect. *Calyptridium*, with eight species in North America, is not only related to other members of *Cistanthe* (Carolin, 1987; also implicit in Nilsson, 1967, and Nyanyano, 1986, 1990) but is also cladistically inextricable from the remainder of the genus (see above). Also significant is the recognition of the relationship of the Cascade-endemic *C.* (*Strophiolum*) *tweedyi* (A. Gray) Hershkovitz to *Cistanthe* (Hershkovitz, 1990b, in press b). Finally, the realization that *Cistanthe guadalupensis* (Dudley in D. Jordan) Carolin ex Hershkovitz (Guadalupe Island) belongs in *C.* sect. *Cistanthe* (Carolin, 1987; Hershkovitz, 1990a) rather than *Talinum* (Dudley, 1899) contributes an additional species to the North American element of *Cistanthe*. The misassignment of this species to *Talinum*, perpetuated in all pre-Carolin (1987) taxonomic treatments (e.g., Rydberg, 1932; Pax & Hoffmann, 1934; Wiggins, 1980), yielded a spurious interpretation of the distribution of *Talinum* (cf. Raven & Axelrod, 1978: 38).

Although the bulk (ca. 35 spp.) of *Cistanthe* remains South American, the degrees of morphological variation, ecological specialization, and geographical extent among the North American species are comparable. The diversity and distinctiveness of North American *Cistanthe* would not corroborate hypotheses that these species are either all recent immigrants from South America or descendants from a single common ancestral immigrant. *Cistanthe maritima* and *C. guadalupensis* may, in fact, represent relatively recent arrivals—these species are morphologically very similar to South American members of sect. *Cistanthe*, and both have very limited distributions in open, hence invasible, coastal habitats. Because of its morphological distinctiveness, *C. ambigua* fails to fit the profile of a recent immigrant (see above). *Cistanthe* sects. *Calyptridium* and, especially, *Strophiolum* are also morphologically distinct from their North and South American counterparts. The possibility that sect. *Strophiolum* represents the sister group to the remainder of the genus is particularly significant, because it implies that *Cistanthe* was present at least as early in North America as, if not earlier than, in South America. Overall, no simple biogeographic scenario emerges to account for the diversity and distribution of North American *Cistanthe*.

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LEAF MORPHOLOGY OF *CISTANTHE* SPACH (PORTULACACEAE)[1]

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ABSTRACT

Leaves of *Cistanthe* are typically characterized by broad, more or less clasping leaf bases, winged petioles, festooned brochidodromous venation, apically diminished primary veins, sinuous veins, "ribbonlike" veins, and predominantly brachyparacytic and similar stomata. This particular combination of characteristics does not occur in any other taxa in Portulacaceae, although most of the traits occur in individual species of *Rumicastrum*. Leaf morphology is similar in all sections of *Cistanthe* except for the monotypic sect. *Strophiolum*, which lacks sinuous veins and ribbonlike veins. Individual species may, however, possess distinctive foliar traits or combinations of traits. Overall, the leaf morphological evidence corroborates the hypothesis of monophyly of *Cistanthe*, but does not substantially clarify the phylogenetic position of this genus, nor relationships therein. Leaf characters may have utility for additional phylogenetic study.

Although the systematic foliar morphology of the dicotyledons remains poorly surveyed compared to reproductive morphology, its potential for providing phylogenetic information is becoming increasingly appreciated (see, e.g., Gifford & Foster, 1989). Instrumental in the apparent resurgence of foliar morphological study was the refinement of the classification of foliar features, especially for venation pattern (Hickey, 1973) and stomatal features (for review, see Baranova, 1987). When studied in light of the more sophisticated terminology, leaves revealed long-overlooked features that have contributed considerably to the understanding of angiosperm origins and phylogenetic trends (Hickey & Wolfe, 1975). The classification of venation features, in particular, has occasioned analyses of foliar morphology in familial and subfamilial taxonomic studies, for example, by Gillespie (1988) for *Omphalea* (Euphorbiaceae); Keating & Randrianasolo (1988) for Rhizophoraceae; Levin (1986a, b, c) for Phyllanthoideae (Euphorbiaceae); Dickison (1975) for Cunoniaceae; Todzia (1988) for *Hedyosmum* (Chloranthaceae); and others (see Levin, 1986a). Some studies (especially Levin, 1986c) used leaf characters in cladistic analyses, which permitted evaluation of the significance of foliar evolution during the course of phylogeny.

Despite the relative technical simplicity of leaf morphological investigation, systematic studies of Portulacaceae have heretofore made limited use of foliar features. The first detailed and extensive survey of foliar features in the family was by Becker (1895), who studied leaf histology, stomatal morphology, and trichomes in more than 30 species. The systematic significance of trichomes in Portulacaceae was subsequently considered by Chorinsky (1931), Franz (1908), Pax & Hoffmann (1934), and Reiche (1897, 1898). Later, Kelley (1973; see Carolin, 1987, in press; Hershkovitz, 1990a, 1991c) surveyed essentially all species of *Calandrinia* s.l. for trichome morphology. McNeill (1975), in his numerical phenetic analysis of the tribe Montieae, incorporated gross leaf and epidermal features in the database. Hershkovitz (1986) presented a preliminary assessment of leaf venation patterns and their potential taxonomic significance in Portulacaceae. Nyanyano (1986a, b, 1988) described stomata, trichomes, and leaf bundle sheath anatomy in ca. 100 species of Portulacaceae. Carolin (1987), in his phylogenetic analysis of Portulacaceae, included three trichome characters in the database. Otherwise, foliar features have been used primarily in monographs, revisions, and floristic treatments of various Portulacaceae, e.g., by

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Nilsson (1966, 1967, 1970, 1971a, b) for Montieae, Reiche (1898) for Chilean *Calandrinia* s.l., and Rydberg (1932) for several genera.

For various reasons, the use of foliar characters in these studies did not significantly advance the understanding of taxonomic relationships among Portulacaceae. For example, the most distinctive of the observed traits, multicellular trichomes and "kranz" vascular bundles, have a highly restricted incidence in the family and occur in species that were already regarded as closely interrelated (Kelley, 1973; Nyanyano, 1986a, 1988; Reiche, 1897, 1898). Carolin (1987), however, misscored some OTUs for trichome characters, which may have contributed, at least partially, to some spurious results (Hershkovitz, 1990a, in press a, in press b). The stomatal data (Nyanyano, 1986a, b) was interpreted according to Metcalfe & Chalk's (1950) simplistic scheme that recognizes few basic stomatal types. All but Carolin's (1987) study were executed using "pre-cladistic" taxonomic concepts. As a result, the monophyly of existing supraspecific taxon circumscriptions was not seriously questioned, and interpretations of variation did not incorporate the concepts of character polarity and parsimony. Thus, my earlier interpretations of leaf venation pattern evolution in Portulacaceae (Hershkovitz, 1986) reflected not only inadequate sampling, but also unnatural generic and tribal circumscriptions. The monographic and floristic considerations of foliar characters emphasized primarily species delimitations rather than interrelationships.

The present work, which stems from my preliminary survey of leaf venation patterns in Portulacaceae and represents a revision of a chapter of my dissertation (Hershkovitz, 1990a), provides a systematic characterization of gross leaf morphology, leaf venation pattern, and leaf epidermal morphology of *Cistanthe* Spach. *Cistanthe* consolidates ca. 47 species of temperate western North America and South America that had formerly been classified in as many as five genera and four tribes (Hershkovitz, 1990a, b, 1991c). Five sections of *Cistanthe* are recognized here (see Hershkovitz, 1990a, b, 1991c; cf. McNeill, 1974), including *C.* sect. *Cistanthe*, *C.* sect. *Amarantoideae* (Reiche) Carolin ex Hershkovitz, *C.* sect. *Philippiamra* (Kuntze) Hershkovitz, *C.* sect. *Calyptridium* (Nutt. in Torrey & A. Gray) Hershkovitz, and *C.* sect. *Strophiolum* (B. Mathew) Hershkovitz. Carolin (1987), in his cladistic analysis of Portulacaceae, determined that the first four of these formed a monophyletic grouping (Fig. 1) evidenced by the nearly universally shared presence of unequal inflorescence bracts. *Cistanthe* sect. *Strophiolum* was later cladistically associated with this group rather than *Lewisia*, based in part on its possession of unequal inflorescence bracts (Fig. 2; Hershkovitz, 1990a, in press c). Elsewhere, I have described the leaf morphology of sect. *Strophiolum* (Hershkovitz, 1990a, in press c) and discussed relationship among the sections of *Cistanthe* and of this genus to other Portulacaceae (Hershkovitz, 1990a, 1991c).

The purpose of such a detailed consideration of leaf morphology in *Cistanthe* is severalfold. First, this study seeks to establish whether the circumscription of the genus, itself representing a radical departure from pre-Carolin (1987) taxonomies of Portulacaceae, receives support from leaf evidence. Second, by defining leaf characters and evaluating character states in *Cistanthe*, this study contributes to the database that can be used for resolving phylogenetic relationships within the genus and of this genus to other Portulacaceae. Third, the data presented in this study contribute to the existing body of information on foliar morphological phenomena and is thus potentially useful for studies of foliar morphological evolution, of the relationship between leaf form and function, and of leaf morphogenesis.

Materials and Methods

1. gross leaf morphology

Gross leaf morphological variation of *Cistanthe* was surveyed primarily from herbarium specimens and described according to the terminology proposed by Dilcher (1974) and Hickey (1971, 1973, 1979). Figures 3–21 illustrate the range of variation in gross leaf morphology in *Cistanthe*; Figures 22–38 illustrate the gross morphology of the leaf apices. These illustrations are arranged according to sectional taxonomy. Table 1 lists vouchers, putative identifications, and full taxonomic citations of all specimens examined for anatomical features. Table 1 also lists additional representative specimens of North American *Cistanthe* examined for gross leaf morphology. I have provided elsewhere a listing of ca. 175 representative collections and putative determinations of South American *Cistanthe* (Hershkovitz, 1991a) and of specimens of *Cistanthe* (*Strophiolum*) *tweedyi* examined for leaf morphology (Hershkovitz, 1990a, in press c).

2. leaf venation pattern

Leaf venation was examined in ca. 250 cleared leaves representing essentially all species of *Cistanthe* and all leaf sizes and shapes in the genus.

TABLE 1. Specimens examined for leaf morphology. Listed below by section are specimens of *Cistanthe* that were examined for leaf morphology, including vouchers of specimens illustrated and/or cited in the present paper. Additional specimens of South American species examined only for gross leaf morphology are listed elsewhere (see Hershkovitz, 1991a), as are specimens of *Cistanthe* sect. *Strophiolum* (see Hershkovitz, in press c). Representative specimens of North American species examined only for gross leaf morphology are denoted below with an asterisk (*). Specimens examined for epidermal morphology but not venation pattern are denoted with a dagger (†). The remaining specimens were sampled for leaf venation studies and some also for epidermal morphology (see Table 2). Identifications are revised from Hershkovitz (1990a) and remain tentative (see Hershkovitz, 1991a).

Cistanthe sect. *Amarantoideae* (Reiche) Carolin ex Hershkovitz, Phytologia 68: 269. 1990 ("*Amarantoides*").

Cistanthe ambigua (S. Watson) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. U.S.A. CALIFORNIA: *M. E. Jones s.n.* (UC); *Munz 9982* (UC); *Nelson & Nelson 3287* (US).

Cistanthe calycina (Philippi) Carolin ex Hershkovitz, Phytologia 70: 220. 1991. CHILE. ANTOFAGASTA: *Johnston 3590* (US); *Johnston 5318* (US). ATACAMA: *Werdermann 418* (US).

Cistanthe densiflora (Barnéoud in Gay) Hershkovitz, Phytologia 70: 220. 1991. ARGENTINA. SAN JUAN: *Cabrera 29553* (US); *Castellanos 15520* (US).

Cistanthe salsoloides (Barnéoud in Gay) Carolin ex Hershkovitz, Phytologia 70: 221. 1991. CHILE. ANTOFAGASTA: *Werdermann 1048* (*leg. Francke*; F, US).

Cistanthe sect. *Calyptridium* (Nutt. in Torrey & A. Gray) Hershkovitz, Phytologia 68: 267. 1990.

Cistanthe monandra (Nutt. in Torrey & A. Gray) Hershkovitz, Phytologia 68: 267. 1990. MEXICO. SONORA: *Wiggins 8193* (US). U.S.A. ARIZONA: *Harris 1477* (US); *Toumey s.n.* (US). CALIFORNIA: *Heller 7641* (US)*.

Cistanthe monosperma (E. Greene) Hershkovitz, Phytologia 68: 267. 1990. U.S.A. CALIFORNIA: *Elmer 3733* (US)†; *Heller 10804* (US).

Cistanthe parryi (A. Gray) Hershkovitz, Phytologia 68: 268. 1990.

Cistanthe parryi var. *arizonica* (J. T. Howell) Kartesz & Gandhi, Phytologia 71: 62. 1991. U.S.A. ARIZONA: *Griffiths 3556* (US).

Cistanthe parryi var. *hessae* (J. H. Thomas) Kartesz & Gandhi, Phytologia 71: 62. 1991. U.S.A. CALIFORNIA: *Thomas & Ernst 6001* (US)*.

Cistanthe parryi var. *nevadensis* (J. T. Howell) Kartesz & Gandhi, Phytologia 71: 62. 1991. U.S.A. NEVADA: *Beatley 5732* (US).

Cistanthe parryi var. *parryi*. U.S.A. CALIFORNIA: *Munz 5726* (UC)*; *Parrish 3081* (UC)*; *Parrish 3725* (US); *Peirson 3124* (UC)*.

Cistanthe pulchella (Eastw.) Hershkovitz, Phytologia 68: 268. 1990. U.S.A. CALIFORNIA: *Congdon s.n.* (US); *Hamon 80-64* (UC)*; *Hamon 80-19A* (UC)*; *Hoover 3442* (US).

Cistanthe pygmaea (Parish ex Rydberg) Hershkovitz, Phytologia 68: 268. U.S.A. CALIFORNIA: *Howell 17427* (CAS)*; *Parish 1803* (holotype, CAS)*; *Twisselmann 16891* (CAS)*.

Cistanthe quadripetala (S. Watson) Hershkovitz, Phytologia 68: 268. 1990. U.S.A. CALIFORNIA: *Baker 3075* (UC)†; *Hoover 3571* (US); *Parish 3082* (US); *Sharsmith 4345* (US).

Cistanthe rosea (S. Watson) Hershkovitz, Phytologia 68: 268. 1990. U.S.A. CALIFORNIA: *Alexander & Kellogg 4352* (US); *Duran 2805* (US); *Reveal & Reveal 424* (UC)*. OREGON: *Cusick 2585* (US).

Cistanthe umbellata (Torrey) Hershkovitz, Phytologia 68: 268. 1990. U.S.A. CALIFORNIA: *Heller 12062* (US); *Jones 2460* (US). OREGON: *Abrams 11351* (US); *Coville & Applegate 422* (US).

Cistanthe sect. *Cistanthe*

Cistanthe arenaria (Cham.) Carolin ex Hershkovitz, Phytologia 70: 211. 1991. CHILE. COQUIMBO: *Wagenknecht 18444* (F, UC). ÑUBLE: *Joseph 3990* (US).

Cistanthe cephalophora (I. M. Johnston) Carolin ex Hershkovitz, Phytologia 70: 212. 1991. CHILE. ANTOFAGASTA: *Werdermann 855* (US).

Cistanthe coquimbensis (Barnéoud in Gay) Carolin ex Hershkovitz, Phytologia 70: 212. 1991. CHILE. COQUIMBO: *Werdermann 881* (F).

Cistanthe cymosa (Philippi) Hershkovitz, Phytologia 70: 213. 1991. CHILE. ANTOFAGASTA: *Werdermann 853* (US); *Worth & Morrison 15816* (NA).

Cistanthe fenzlii (Barnéoud in Gay) Carolin ex Hershkovitz, Phytologia 70: 213. 1991. CHILE. BIO-BIO: *Neger s.n.* (M); *Philippi s.n.* (B).

Cistanthe grandiflora (Lindley) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. CHILE. ACONCAGUA: *Morrison et al. 16872* (NA); *West 3959* (F, UC, US). ANTOFAGASTA: *Worth & Morrison 16133* (NA). ATACAMA: *Werdermann 405* (F, UC). BIO-BIO: *Hutchinson 234* (UC, US). COQUIMBO: *Zollner 10284* (NA). U.S.A. CULTIVATED: *Peele 154* (NA).

Cistanthe guadalupensis (Dudley in D. Jordan) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. MEXICO. GUADALUPE IS.: *Lindsay 2635* (UC)*; *Moran 5991* (US)*; *Wiggins & Ernst 174* (UC).

Cistanthe lingulata (Ruíz Lopez & Pavón) Hershkovitz, Phytologia 70: 214. 1991. PERU. ANCASH: *Ferreyra 13532* (US). LA LIBERTAD: *López Miranda 374* (US). LIMA: *Ferreyra 10486* (US).

Cistanthe longiscapa (Barnéoud in Gay) Carolin ex Hershkovitz, Phytologia 70: 215. 1991. CHILE. ATACAMA: *Johnston 5034* (US); *Werdermann 445* (F).

Cistanthe maritima (Nutt. in Torrey and A. Gray) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. MEXICO. ESTADO DE BAJA CALIFORNIA: *Bacigalupi 3045* (UC); *Webster 21615* (DAV)*; *Wiggins & Ernst 207* (UC).

Cistanthe paniculata (Ruíz Lopez & Pavón) Carolin ex Hershkovitz, Phytologia 70: 216. 1991. PERU. AREQUIPA: *Ferreyra 12022* (US).

Cistanthe picta (Gillies ex Arn. in Cheek) Carolin ex Hershkovitz var. *picta*, Phytologia 70: 217. 1991. CHILE. ACONCAGUA: *Hutchinson 98* (US). ATACAMA: *Johnston 6218* (US). METROPOLITANA: *Kuntze s.n.* (US); *Morrison et al. 16786* (NA)†. O'HIGGINS: *Pennell 12279* (F).

Cistanthe picta var. *frigida* (Barnéoud in Gay) Hersh-

TABLE 1. Continued.

kovitz, Phytologia 70: 218. 1991. CHILE. COQUIMBO: *Morrison et al. 16992* (NA).

Cistanthe weberbaueri (Diels) Carolin ex Hershkovitz, Phytologia 70: 218. 1991. PERU. AREQUIPA: *Ferreyra 12006* (US). LIMA: *Weberbauer 5321* (F).

Cistanthe sp. cf. *C. arenaria*. CHILE. COQUIMBO: *Zollner 10636* (NA; the smaller-leaved specimens of this mixed collection—see Hershkovitz, 1991a). METROPOLITANA: *Joseph 2785* (US—see Hershkovitz, 1991a).

Cistanthe sp. cf. *C. longiscapa*. CHILE. ATACAMA: *Worth & Morrison 16184* (NA; see Hershkovitz, 1991a).

Cistanthe sp. CHILE. COQUIMBO: *Zollner 9807* (NA; see Hershkovitz, 1991a).

Cistanthe sect. *Philippiamra* (Kuntze) Hershkovitz, Phytologia 68: 269. 1990.

Cistanthe celosioides (Philippi) Carolin ex Hershkovitz, Phytologia 68: 269. 1990. CHILE. ANTOFAGASTA: *Biese 613* (UC); *Werdermann 862* (UC, US); *West 3859* (UC); *Worth & Morrison 15820* (UC). ATACAMA: *Werdermann 477* (US).

Leaves of herbarium (rarely ethanol-preserved) specimens were cleared by successive treatments with Fisher Aerosol OT, ca. 10% aqueous sodium hydroxide, and 200% aqueous chloral hydrate, and stained with 1% basic fuchsin in 100% ethanol. The leaves were destained as necessary in ca. 70% ethanol, dehydrated, and mounted in standard media (e.g., Fisher Permount) using appropriately sized glass slides and cover slips. Prior to mounting, selected specimens were counterstained in ca. 0.1% fast green in 1 : 1 absolute ethanol : xylene. Gross venation patterns illustrated in Figures 3–54 were photographed by inserting the cleared leaf specimen into a photographic enlarger, sometimes with a green acetate filter, and projecting the image on photographic paper. Highly magnified venation details were photographed using a compound microscope and brightfield optics sometimes enhanced with variable degrees of Nomarski interference. The optimal preparatory regimen and photographic technique varies with the taxon, and additional information may be obtained upon request.

Venation is described according to the "Hickey system" (Dilcher, 1974; Hickey, 1971, 1973, 1979; Hickey & Wolfe, 1975). I follow Levin (1986a), however, in consistently referring to brochidodromous and higher-order "loops," rather than "arches" and loops (cf. Hickey & Wolfe, 1975). The Hickey system was undoubtedly inspired by, and best adapted to, leaves of taxa having large numbers of "iterations" of architectural features, especially those of woody perennials that bear numerous (hundreds to many thousands of) leaves having more or less uniform morphology, and in which particular venation features are repeated many times in each leaf. Members of *Cistanthe*, however, like most Portulacaceae, are herbaceous perennials and annuals, bearing few (sometimes only 10–20) leaves per season or lifetime, and the major leaf venation features iterate relatively few times. The paucity of leaves per plant can increase the degree of morphological variance in the sample because of heteroblasty. Likewise, the paucity of regularly iterated venation features within a leaf results in greater morphological variance among the iterations. As a result, attempting to discern a leaf architectural "mode" for a species of *Cistanthe* is difficult. Nevertheless, the Hickey system, because of its classification of a large number of venation details, provides a useful framework for the present discussion.

3. EPIDERMAL MORPHOLOGY

Epidermal morphology was examined in more than 37 specimens representing ca. 20 species or species complexes (i.e., including segregate species elsewhere recognized; see Hershkovitz, 1991a) of *Cistanthe*. Emphasis in this study is on the morphology of the stomatal complex on the abaxial intercostal region. Figures 80–94 illustrate the epidermal morphology of selected species. Table 2 provides brief descriptions for all examined specimens, which are vouchered in Table 1. Epidermal peels were obtained from herbarium specimens by treating leaf fragments successively with ca. 10% sodium hydroxide, distilled water, 30% hydrogen peroxide, FAA, and 50% ethanol. This harsh procedure readily separates the abaxial epidermal layer from the mesophyll, although often part or all of the adaxial epidermis is separated as well. Epidermal tissue from the abaxial intercostal region was studied on wet-mounts and subsequently preserved in 50% ethanol. Epidermal peels were photographed using brightfield optics with variable degrees of Nomarski interference. The optimal preparatory regimen and photographic technique varies with the taxon, and additional information may be obtained upon request.

RESULTS

1. GROSS LEAF MORPHOLOGY

Leaves of *Cistanthe* are simple, entire, and somewhat to quite succulent, although the precise degree of succulence could not be determined from herbarium material.

The typical leaf area in different species varies

from less than 10 mm² (*C. picta* var. *frigida*, Fig. 55; and *C. pulchella*), to over 3,000 mm² (*C. grandiflora*; *C. paniculata*, Fig. 3; *C. tweedyi*, see Hershkovitz, 1990a, in press c). According to the leaf area classes defined by Dilcher (1974), the leaf area in *Cistanthe* ranges from microphyllous to mesophyllous.

The leaf shape in species of *Cistanthe* ranges from approximately wide obovate (Figs. 3–6), through narrow oblanceolate (Figs. 12, 14, 19), to essentially linear and/or terete (Figs. 13, 18). The lamina may be essentially straight and symmetrical (Figs. 8, 9, 20) to more often asymmetrical, and slightly curved to S-shaped (Fig. 10). Leaf symmetry usually varies in a species or individual.

The shape of the leaf apex may be acute (Figs. 8, 9, 27), acuminate (Fig. 37), to rounded (Figs. 25, 26, 34), and weakly emarginate (Fig. 17) to weakly mucronate (Fig. 24). Characterization of leaf apex shape is sometimes relative to the point of reference; for example, the leaf shown for *C. weberbaueri* (Figs. 10, 28) is more or less acuminate toward the apex, but rounded at the very tip.

Petiolar development varies in the genus. Typically an individual will have distinctly petiolate and essentially sessile leaves, along with leaves of intermediate morphology. Leaf bases in petiolate leaves constrict more abruptly (Fig. 6) than gradually. Such leaves appear to be differentiated into an elliptical, ovate, orbicular, rhombic, or lanceolate blade portion, and a narrower, winged, petiole portion. In petiolate and sessile leaves, the leaf base broadens at the point of attachment to the stem so that it is nearly or quite clasping. Amplexicaul leaves occur in Peruvian plants that have been referred to *C. paniculata* (Hershkovitz, 1991a).

While the leaves illustrated here more or less typify the species or species complexes shown, the variability is such that putatively closely related species exhibit no obvious consistent distinctions in gross leaf morphology. Likewise, no distinctions among the sections of *Cistanthe* are evident, except to the degree that the more polymorphic sections (i.e., those with more species) vary more than the less polymorphic. Not all species intergrade, however; leaves of *Cistanthe grandiflora*, *C. picta*, *C. ambigua*, and *C. quadripetala*, for example, are readily distinguishable from one another.

2. LEAF VENATION PATTERN

The venation features of *Cistanthe* (except for sect. *Strophiolum*, described and illustrated in Hershkovitz, 1990a, in press c) are selectively illustrated in Figures 3–79. These illustrations are arranged according to subject, from gross venation pattern to finer anatomical details. Within each grouping, illustrations are arranged according to sectional taxonomy.

Because of the apparent variation in gross leaf morphology in species or species complexes, the concomitant variation in venation features, the paucity of iterated venation features in individual leaves, and the difficulties encountered in identifying material (see Hershkovitz, 1991a), useful and reliable descriptions of venation in individual species was largely unobtainable. The descriptions presented here emphasize the venation features characteristic of *Cistanthe* as a whole and the distribution and range of variation of these features. Particular features encountered in only a few taxa are also noted.

Venation type. Venation in *Cistanthe* is usually irregularly festooned brochidodromous (Figs. 3–11, 15–17, 20, 21, 39–46, 50, 51, 53, 54; cf. Hickey & Wolfe, 1975: 547, fig. 5), sometimes only weakly festooned (Figs. 12, 19, 47, 52), less often irregularly brochidodromous with only a hint of festooning (Figs. 13, 14, 48, 49). (See also discussion of secondary veins, below.)

Primary vein. The primary vein is prominent basally (but more so in some taxa than in others; e.g., compare Figs. 13, 17) and much diminished to obsolete apically (Figs. 22–38). The primary vein may be evident as a protruding veinlet at the leaf tip (Figs. 24, 27, 29) or not at all evident at the apex (Figs. 25, 26). Hickey's (1973) parameter for primary vein size—relative width midway between the blade base and apex—cannot be satisfactorily evaluated in *Cistanthe*, because the blade is not readily definable (see above). The primary vein course varies, but usually shows a slight zigzag or angular shift in course away from the departing secondary veins (Figs. 6, 15, 55). (See also comments on general vein course, below.)

Secondary veins. Prominent secondary veins are generally few—three to four pairs per leaf—and their number is apparently not strongly correlated with leaf size (e.g., compare Figs. 6, 55). The basalmost secondary veins are often less prominent and more decurrent or more acutely angled than the apical secondaries. The secondary veins generally change course abruptly and form loops with suprajacent secondary veins. These secondary loops are often situated one-half to two-thirds the distance from the primary vein to the leaf margin in broader leaves (Figs. 3–6) and proportionally closer to the leaf margin in narrower leaves (Fig. 10). Sometimes secondary loops fail to form or form only weakly in leaves otherwise possessing

such loops (Figs. 15–17). Tertiary loops are barely evident in the narrowest leaves (Figs. 48, 49) but are present, sometimes along with 4° and 5° loops, in broader leaves (Figs. 39–46, 50–54).

Intersecondary veins. Simple intersecondary veins are sometimes present in the intercostal regions, especially in broader leaves (Figs. 4–7, 10, 11, 20, 21).

Tertiary veins. Tertiary veins are irregularly developed, variable in size, and, because of intergradation in prominence between lower and higher vein orders, sometimes difficult to identify throughout the leaf. Those arising from the apical side of the secondary veins are generally more prominent than those arising from the basal side. The branch angle varies but is generally more acute on the apical side of the secondary veins than the basal. The tertiary vein pattern is ramified to reticulate but sometimes varies in different parts of the same leaf. Rarely, the tertiary veins are nearly percurrent (Fig. 16).

Higher-order veins (excluding freely ending veinlets). In the smallest and/or narrowest leaves, the highest vein order is essentially equivalent to the tertiary veins (Figs. 47–49, 55). In the largest leaves, a fourth order of veins is present. Fourth-order veins are not always readily distinguishable as such throughout the lamina because ramifications of the tertiary veins can be highly variable in prominence. Fourth-order veins, tentatively identified as such in Figures 39–43, 45, 46, 50, 51, 53, 54, are usually ramified or rarely more orthogonally reticulate, as in *C. longiscapa* (Fig. 40). Fifth-order veins are rarely distinguishable as such, e.g., in *C. paniculata* (Fig. 39), *C. longiscapa* (Fig. 40), and *C. monosperma* (Fig. 51).

Marginal venation. The marginal venation ranges from incomplete (Figs. 42, 44) to somewhat looped (Fig. 39) but is usually intermediate between these forms.

Freely ending veinlets. The freely ending veinlets are highly variable in length and degree of branching (Figs. 56–67) and may be prominently dilated with respect to the penultimate veins (Figs. 64–66) or hardly dilated at all (Fig. 60). The veinlets are sometimes distally coalesced with adjacent veinlets and/or veinlet branches (Figs. 56, 61–63). The terminal tracheary elements of the dilated veinlets are usually numerous, short, and densely clustered. Similarly short tracheary elements ("tracheoids") also occur rarely along the highest-order veins (Fig. 56). The terminal elements of the less dilated veinlets are more elongate and less densely clustered (Figs. 60, 67).

Areoles. Areoles are difficult to define in *Cistanthe* because the vein orders are not well differentiated, but they are probably best characterized as imperfect to incomplete, and least well developed in the smaller or narrower leaves (Figs. 48, 49, 55). Hickey's illustration of "incomplete" areolation (1979: 37, fig. 117) shows local differences in venation density. Such differences are generally not present in larger leaves of *Cistanthe*, in which the venation is more or less uniformly dense, although the shape and size of ultimate enclosures in a leaf are highly variable (Figs. 56–61). The number of veinlets per ultimate enclosure is typically 0–2 but may be more in the elongate enclosures that adjoin major veins.

Other venation features

a. Vein course. The veins are sinuous in most or all vein orders in most species, although individuals of some species may have less sinuous or straight veins, especially in *C. umbellata* (Fig. 16), *C. monosperma* (Figs. 17, 51), *C. tweedyi* (Hershkovitz, 1990a, in press c), and in some leaves and/or higher vein orders of *C. picta* (Fig. 58). Sinuous venation is possibly an artifact of specimen shrinkage during drying or preparation, but it nevertheless represents a diagnostic trait because similarly prepared leaves of other succulent-leaved members of Portulacaceae do not have sinuous veins (e.g., *Lewisia* spp.; Hershkovitz, in press c).

b. Three-dimensional venation. A few species of *Cistanthe* have veins that interconnect in more than one plane, i.e., have three-dimensional venation. Three-dimensional venation occurs in leaves that are especially succulent but not necessarily more succulent than leaves with two-dimensional (planar) venation. In the *C. grandiflora* complex (see Hershkovitz, 1991a), the finer veins in the central and basal portion of the leaf blade form a complex three-dimensional network (Fig. 68). In *C. paniculata*, the fine veins in the central and basal portion of the leaf blade may form a planar reticulum adaxial to the plane of the major veins (Fig. 69). In the cylindrical leaves of *C. ambigua*, the primary vein occurs toward the adaxial surface, and the departing veins follow the contour of the leaf toward the abaxial surface (Figs. 18, 35, 70). Toward the leaf apex, the marginal venation interconnects abaxially, forming a basketlike reticulum.

c. Vein density. Gibson (1982) estimated the density of venation by dividing the number of vascular bundles present in a leaf cross section by the length of the section, and by measuring the distance between bundles. He observed that vein density is much lower in succulent leaves of desert perennials

than in nonsucculents. Vein density in members of *Cistanthe*, which are succulent, was here estimated by counting the number of veins crossing arbitrarily delimited transects of the photographs in Figures 39–54 and dividing by the length of the transect, yielding data equivalent to that obtained by Gibson's method. *Cistanthe grandiflora* (Fig. 44) was not measured because of its extensive three-dimensional venation. The density values averaged slightly less than 5 veins/mm and were mostly lower than the 7 veins/mm minimum reported by Gibson for nonsucculent desert perennials. The highest value observed in *Cistanthe* was ca. 9.5 veins/mm in the small, linear leaves of *C. fenzlii* (Fig. 49). The lowest values, ca. 2.5 veins/mm, were found in *C. paniculata* (Fig. 39) and *C. quadripetala* (Fig. 50).

d. Tracheary element wall pitting. Mostly helical but also annular, scalariform, and reticulate wall thickenings occur (see also below). Scalariform to reticulate thickenings predominate in vessel elements in the primary (and sometimes higher-order) veins of some species (e.g., *C. lingulata*, Fig. 71, and *C. ambigua*, Fig. 72), whereas helical thickenings predominate in the prominent veins of others.

e. Vein anatomy. The finer veins in most species of *Cistanthe* are flat, or "ribbonlike" (Figs. 73–79). These veins are often sinuous and usually one cell-layer thick and up to eleven (perhaps more) tracheary elements wide (Fig. 76). The elements on one side have annular wall thickenings, and those toward the other have progressively less steep helical and, in some cases, scalariform (Fig. 75) to nearly reticulate (Fig. 74) thickenings. Some of the more prominent veins may also be ribbonlike but are more than one cell-layer thick and approach the "normal" condition in vascular plants, in which the tracheary elements are arranged in clusters rather than ribbons and have more or less the same type of secondary wall thickening throughout the vein. Ribbonlike veins appear to be common and characteristic of essentially all the fine veins in some taxa (e.g., *C. quadripetala*, Fig. 60) or relatively rare or absent among the fine veins of others (e.g., *C. picta*, Fig. 58, and *C. umbellata*, Fig. 61). They are absent in sect. *Strophiolum* (Hershkovitz, 1990a, in press c). Ribbonlike leaf veins apparently have not been described in any other vascular plants.

3. VARIABILITY IN VENATION FEATURES

A thorough analysis of the infraspecific variation in venation features of putative species of *Cistanthe* was not undertaken in the present investigation because of poorly defined species limits and the large amount of herbarium material needed for such a study. The limited sampling, however, suggested constancy of venation features in some taxa. This is demonstrated by a comparison of large and small leaves of *C. picta* (Figs. 6, 55), *C. grandiflora* (Figs. 8, 9), and the *C. umbellata* species complex (Figs. 16, 17; see Hinton, 1975). The illustrations show that the larger and smaller leaves of each pair resemble each other more than either does similar-sized leaves of other species (although no other leaves as small as that shown in Fig. 55 are illustrated).

The leaves of *C. grandiflora* appear distinguishable by the co-occurrence of the following traits: (1) a small protrusion of the weakened primary vein at the apex (Fig. 27); (2) relatively fine secondary veins and vein loops, the latter forming proximal to the primary vein; (3) a relatively narrow ($< 30°$) secondary vein angle; (4) prominently dilated terminal veinlets, often juxtaposed with extremely fine penultimate veins; and (5) three-dimensionally reticulating veins in the central and basal portion of the leaf.

Leaves of members of the *C. umbellata* complex are distinguishable on the basis of: (1) primary veins that are particularly prominent toward the leaf base and nearly to quite obsolete at the apex; (2) prominent secondary veins, some of which are prominently looped while others are ramified and not looped; (3) numerous festooning loops; (4) relatively well developed third and fourth vein orders; and (5) a paucity of sinuous veins and ribbonlike veins.

The venation of the leaf of *C. picta* shown in Figure 55 does not closely resemble that of the larger counterpart (Fig. 6). Nevertheless, the former appears to resemble the latter more than it does any other leaf shown in Figures 3–21 because of: (1) the massiveness of the primary vein toward the base and its obsolescence at the apex; (2) the zig-zagging character of the primary vein; (3) the relatively broad angle of the secondary veins; and (4) the paucity of sinuous and ribbonlike veins. Note that venation in *C. picta* is similar to that in the *C. umbellata* complex but has less regularly festooned loops and apparently broader secondary vein angles. Preliminary measurements also indicate a greater vein density in *C. picta* (6–7 veins/mm) than in comparable leaves in the *C. umbellata* complex (3.5–5.5 veins/mm).

In all of the cases described above, the smaller leaves differ from the larger leaves primarily in having lower "rank" (Hickey, 1971); i.e., the higher vein orders and, concomitantly, higher orders

of festooning loops are less or not distinguishable in the smaller leaves.

4. EPIDERMAL MORPHOLOGY

a. Stomatal morphology. Nyanyano (1986a, b) referred to stomata in *Cistanthe* sects. *Calyptridium* and *Philippiamra* as paracytic. Nyanyano (1986a) illustrated paracytic stomata in *C.* (*Cistanthe*) *grandiflora*; otherwise his results for *Cistanthe* sects. *Cistanthe* and *Amarantoideae* cannot be determined because he did not report results for individual species, and he included these sections of *Cistanthe* in *Calandrinia* s.l., in which both paracytic and tetracytic stomata were reported. Contrary to what Nyanyano (1986a, b) claimed, his characterizations of stomatal types correspond to the simplistic classification proposed by Metcalfe & Chalk (1950), rather than the more precise classification proposed by Wilkinson (1979), in which different types of paracytic (e.g., brachyparacytic) stomata are distinguished. Becker (1895) also reported the presence of two lateral subsidiary cells (= paracytic s.l.) in sect. *Calyptridium*.

The principal morphological features of stomata in *Cistanthe* are illustrated for several species in Figures 80–94 and diagrammed in Figure 95. Table 2 summarizes stomatal morphology for several specimens vouchered in Table 1. The stomata are described below following Wilkinson's (1979) terminology except as noted.

The most common stomatal type found in *Cistanthe* is brachyparacytic (Fig. 95B), in which the guard cells are flanked by a pair of subsidiary cells but not enclosed by them. The morphology of the lateral subsidiary cells varies: the shape ranges from reniform (i.e., contoured to the shape of the guard cell; Fig. 95I, J) to more rectangular (Fig. 95L, M) to polygonal (Fig. 95O, P). The width of the subsidiary cells ranges from relatively narrow (Fig. 95I, L, O) to broad (Fig. 95J, M, P). The broader cells are intermediate between distinct subsidiary cells and ordinary epidermal cells. A similar range of variation exists when two subsidiary cells are adjacent to a guard cell (Fig. 95K, N, Q), although the outer subsidiary cell is generally broader than the inner. The opposing subsidiary cells in a brachyparacytic stomatal complex may differ in morphology with respect to the variants noted in Figure 95. To some degree, the variation described above might reflect the optical plane of section. More likely, however, a three-dimensional shape analysis will reveal an even greater degree of variation in subsidiary cell morphology.

Infraspecific variation in stomatal type, not reported by Nyanyano (1986a, b), was found in all specimens, although some specimens were more variable than others. Aside from brachyparacytic, the variants in stomatal type include (cf. Wilkinson, 1979): hemiparacytic (Fig. 95A; only one of the guard cells with a distinct subsidiary cell); amphibrachyparacytic (Fig. 95D; two pairs of flanking subsidiary cells); hemi-amphibrachyparacytic (type proposed herein; Fig. 95C; a total of three lateral subsidiary cells); tetracytic (Fig. 95E; two pairs of subsidiary cells, one pair parallel and one pair perpendicular to the long axis of the guard cells); hexacytic (Fig. 95F; similar to the preceding but with two pairs of lateral subsidiary cells); staurocytic or anomotetracytic (Fig. 95G; three to five subsidiary cells surrounding the guard cells); and anomocytic (Fig. 95H; no distinct subsidiary cells present).

In addition, variants more or less intermediate between pairs of the above listed types and having no formal names occur. In one relatively common variant, one lateral subsidiary cell (or two adjacent cells) is divided transversely (Fig. 95R, S). In rare instances, both flanking cells are divided. Although Wilkinson (1979: 100) noted that this type should not be confused with laterocytic stomata, no sharp structural distinction can be made. Such stomata in *Cistanthe* are here arbitrarily designated brachyparacytic with one or both lateral cells split. *Cistanthe* stomata are thus distinguished from those typifying certain *Lewisia* species, in which the guard cells are flanked by four to eight subsidiary cells (Hershkovitz, 1990a, in press c). In another variation, an elongate subsidiary cell perpendicular to the guard cells occurs at one pole but not the other (Fig. 95T). When such cells occur at both poles, tetracytic and hexacytic stomata may be formed.

A character of the stomatal complex that correlates with morphological type is the number of epidermal cells, whether defined as subsidiary cells or not, that directly border the guard-cell pair ("contact cells," cf. Esau, 1977: 94). This character is useful independently of stomatal type because the distinction between subsidiary cells and ordinary epidermal cells is often arbitrary. Because most examined species of *Cistanthe* have predominantly brachyparacytic stomata (or structurally similar types shown in Fig. 95A–F), the number of contact cells is usually four: two lateral subsidiary cells plus one subsidiary or ordinary epidermal cell at each pole. Occasionally, two ordinary epidermal cells border the guard-cell pair at one or, exceptionally, both poles, so that the number of contact cells is five or, less often, six. It seems potentially possible for more than six contact cells to occur in *Cistanthe* (e.g., if both flanking cells

TABLE 2. Epidermal morphology in some species of *Cistanthe*. Listed below are stomatal types and other epidermal features found on the abaxial intercostal area of selected species and specimens of *Cistanthe*. The species are listed according to section, and the vouchers are cited in Table 1. Epidermal morphology of sect. *Strophiolum* is described elsewhere (Hershkovitz, in press c). The stomatal types, described in the text, are listed, with the suffix "-cytic" omitted. The frequency of the stomatal types in the specimens are denoted as follows: ++, common to predominant type; +, present and recurring throughout the specimen; (+), observed but rare and not recurring throughout the specimen. The evaluations are subjective and intended only to show the general pattern of variation in the genus.

Section Species (voucher)	Anomo-	Hemi-brachy-para-	Brachy-para-	Hemi-amphi-brachy-para-	Amphi-brachy-para-	Tetra-
sect. *Amarantoideae*						
C. ambigua (*Nelson & Nelson 3287*)		+	++	++		
C. calycina (*Werdermann 448*)			++			
C. densiflora (*Cabrera 29553*)			++	++		
C. densiflora (*Castellanos 15520*)			+	++	++	
C. salsoloides (*Werdermann 1048*)			+	++	++	
sect. *Calyptridium*						
C. monandra (*Harris 1477*)		+	+	+		
C. monosperma (*Elmer 3733*)			++	++	++	
C. monosperma (*Heller 10804*)		+	+	+	++	+
C. parryi var. *parryi* (*Beatley 5732*)		(+)	++	++	(+)	
C. parryi var. *parryi* (*Parrish 3725*)			++	++		
C. pulchella (*Congdon s.n.*)	+	++	++			
C. quadripetala (*Hoover 3571*)			+			
C. quadripetala (*Sharsmith 4345*)	++	++	+			
C. rosea (*Duran 2805*)	++	++				
C. umbellata (*Abrams 11351*)			++	++	++	+
C. umbellata (*Heller 12062*)			++	++	++	
C. umbellata (*Jones 2460*)		(+)	++	++	(+)	
sect. *Cistanthe*						
C. cymosa (*Werdermann 853*)		++	++			
C. cymosa (*Worth & Morrison 15816*)	+	++	++	++		
C. fenzlii (*Neger s.n.*)	(+)	+	+	+	+	+
C. grandiflora (*Hutchinson 234*)			+	++	++	
C. grandiflora (*Morrison et al. 16872*)			+	++	++	
C. grandiflora (*Peele 154*)	(+?)	(+)	++	++		
C. grandiflora (*Zollner 10284*)			++	++	++	
C. lingulata (*Ferreyra 10486*)		(+)	++	++	++	
C. longiscapa (*Johnston 5034*)	+	++	++			
C. paniculata (*Ferreyra 12022*)			++	++	++	
C. picta var. *picta* (*Kuntze s.n.*)	+	+	+	+	+	+
C. picta var. *picta* (*Morrison et al. 16786*)	+	+	+	+	+	+
Cistanthe sp. cf. *longiscapa* (*Worth & Morrison 16184*)		++	++			
Cistanthe sp. (*Zollner 9807*)			++	+	(+)	+
sect. *Philippiamra*						
C. celosioides (*Werdermann 477*)			++	++	++	
C. celosioides (*Werdermann 862*)			++	++	++	

TABLE 2. Continued.

Hexa-	Stauro-	Split lateral subsidiary cell	3 contact cells	Epidermal cell outline	Comments
		+		orthogonal	
	+			sinuous	
				sinuous	poor specimen
				orthogonal	
				orthogonal	single polar subsidiary cell sometimes present; papillar cells along leaf margin
		+		orthogonal	small sample
		+		orthogonal	single polar subsidiary cell sometimes present; stomata sunken
+	+	+		orthogonal	stomata highly variable; some papillar cells; stomata sunken
		(+)		orthogonal	papillar cells present; stomata sunken
	+	+		orthogonal to arcuate	few papillar cells present; stomata sunken
				orthogonal to sinuous	few papillar cells present; stomata somewhat sunken
	+				small sample; stomata sunken
			(+)	orthogonal	stomata sunken
				orthogonal	papillar cells present; stomata sunken
+	+	+		orthogonal	stomata highly variable; stomata sunken
(+)	(+)	+		sinuous to orthogonal near midrib	single polar subsidiary cell sometimes present; papillar cells present; stomata sunken
				orthogonal	papillar cells present; stomata sunken
				orthogonal	papillar cells present; some stomata sunken
				orthogonal	
+	+	+		orthogonal to sinuous	stomata highly variable; papillar cells present along leaf margin
				orthogonal	
+	(+)	(+)		orthogonal to arcuate	some polar subsidiary cells present
		(+)		orthogonal to sinuous	
(+)				orthogonal	stomata somewhat sunken
		+	(+)	sinuous	other odd stomatal variants present
		(+)	(+)	sinuous	other stomatal variants present
				orthogonal	stomata somewhat sunken; small sample
	+	+	(+)	sinuous	stomata highly variable
	+	+	(+)	sinuous	stomata highly variable
	(+)			orthogonal	large papillar cells present
	+	+	(+)	somewhat sinuous	other stomatal variants present; small papillar cells along leaf margin
				orthogonal	
				orthogonal	

TABLE 3. Stomatal index, stomatal density, and mean stomatal length in selected members of *Cistanthe*. Vouchers are cited in Table 1. For all measurements, (N) = the number of stomata sampled. All measurements are based on photographs.

Section	Species (voucher)	Stomatal index (N)	Stomata/ mm² (N)	Stoma length (μm) [x ± SD (N)]
sect. *Amarantoideae*	*C. ambigua* (*Nelson & Nelson 3287*)	13.6 (22)	100 (37)	21.9 ± 2.2 (20)
	C. salsoloides (*Werdermann 1048*)	11.1 (22)	69 (24)	24.8 ± 2.4 (20)
sect. *Calyptridium*	*C. parryi* var. *parryi* (*Beatley 5732*)	13.7 (44)	144 (101)	27.3 ± 4.2 (20)
	C. quadripetala (*Sharsmith 4345*)	26.7 (34)	157 (55)	26.4 ± 2.5 (20)
	C. umbellata (*Abrams 11351*)	9.5 (23)	240 (48)	23.8 ± 2.0 (20)
sect. *Cistanthe*	*C. cymosa* (*Werdermann 853*)	13.5 (36)	60 (53)	17.8 ± 2.3 (17)
	C. cymosa (*Worth & Morrison 15816*)	15.6 (45)	233 (63)	15.8 ± 1.1 (20)
	C. fenzlii (*Neger s.n.*)	10.7 (52)	203 (78)	25.1 ± 1.9 (20)
	C. grandiflora (*Werdermann 405*)	11.1 (22)	30 (24)	35.1 ± 3.5 (20)
	C. grandiflora (*Worth & Morrison 16133*)	8.8 (29)	23 (36)	35.6 ± 3.3 (20)
	C. picta var. *picta* (*Kuntze s.n.*)	12.3 (33)	250 (45)	19.0 ± 1.0 (20)
	C. lingulata (*Ferreyra 10486*)	13.3 (42)	203 (78)	30.1 ± 1.8 (20)
	C. sp. cf. *longiscapa* (*Worth & Morrison 16184*)	13.3 (20)	115 (33)	15.6 ± 1.9 (20)
C. sect. *Philippiamra*	*C. celosioides* (*Werdermann 477*)	15.2 (12)	139 (12)	22.7 ± 1.69 (11)
	C. celosioides (*Werdermann 862*)	12.4 (11)	111 (15)	17.9 ± 1.48 (9)

are divided and more than one ordinary epidermal cell borders the guard-cell pair at one or both poles), but no more than six cells bordering the guard-cell pair were observed, and this number is rare.

While all examined material of *Cistanthe* possessed some variation in stomatal morphology, the pattern and degree of variation differ among the taxa (see Table 2). The least variation occurred in members of the *C. grandiflora* complex (Fig. 80), in which amphi- and hemi-amphibrachyparacytic stomata predominate, while other types are rare. Relatively little variation also characterizes *C. lingulata* (Fig. 85), *C. salsoloides* (Fig. 90), and *C. celosioides* (Fig. 94). Greater variation occurs in *C. picta* (Figs. 82, 83), *C. fenzlii* (Fig. 84), and *C. umbellata* (Fig. 92). High proportions of hemibrachyparacytic stomata (e.g., *C. cymosa*, Fig. 88) or anomocytic stomata (e.g., *C. quadripetala*, Fig. 91) are uncommon in the genus. "Double" stomata, in which two guard-cell pairs adjoin, were observed in *C. cymosa* and *C. quadripetala* (Figs. 88, 91).

Sunken stomata occur in several taxa (Table 2) and are often variably present in an epidermal specimen. Sunken stomata are most prominent and frequent in sect. *Calyptridium*, e.g., *C. rosea* (Fig. 93) and *C. umbellata* (Fig. 92). Sunken stomata are illustrated in *C. grandiflora* (Fig. 80), *C. longiscapa* (Fig. 81), and *C. cymosa* (Fig. 88).

Biometric stomatal parameters (stomatal index, stomatal density, and stomatal size) were only sporadically surveyed in *Cistanthe* (Table 3). The preliminary data suggest only limited taxonomic utility of these parameters. The stomatal index values are similar to those noted for other angiosperms (cf. Wilkinson, 1979). The lower stomatal densities observed are typical of those found in other succulent-leaved species (cf. Gibson, 1982). Likewise, the stomatal lengths are in the "normal" range found in other plants (cf. Wilkinson, 1979). The stomatal index in *C. quadripetala* is greater than in other species of *Cistanthe*, but the stomatal density and length in *C. quadripetala* are not remarkable. The high stomatal index in this case apparently reflects the high incidence of anomocytic stomata in *C. quadripetala*; i.e., the total number of subsidiary cells will correlate with the ratio of guard cells to subsidiary and ordinary epidermal cells. The correlation between low stomatal density and high stomatal length in the *C. grandiflora* complex has been reported for other xerophytic herbs (Wilkinson, 1979).

Other biometric parameters, including the variation in stomatal index or density on the abaxial versus adaxial surface of the leaf and angle of orientation of the guard cell axis relative to the leaf axis, were not measured. Leaves of *Cistanthe*, like all Portulacaceae, are amphistomatic (cf. Nyanyano, 1986a, b), and the stomatal index and/or density might be expected to be lower on the adaxial surface, although superficial observations of a few adaxial epidermal layers did not indicate

that the difference was marked. In the intercostal region, the guard cell axis appears to be oriented randomly (see Figs. 80–94). No average or modal angle of divergence of the guard-cell axis was calculated here. Toward the leaf midrib, however, the guard-cell axis appeared to be more commonly oriented in the direction of the leaf axis.

b. Stomatal ontogeny. Ontogeny of the stomatal complex was not studied, nor was the precise sequence of cell division generally inferable from the mature stomatal morphology, because it is known that particular structural types of stomata are derivable from different ontogenetic pathways (Farooqui, 1981a, b; Rasmussen, 1981). Superficially, however, ontogeny of the stomatal complex appears to vary in *Cistanthe*. For example, in *C. salsoloides* (Fig. 90), the structure of the stomatal complex suggests mesogenous development, whereas the subsidiary cells of *C. ambigua* (Fig. 89) appear to be mesoperigenous or perigenous. (Payne (1979) doubted whether stomata can be truly perigenous (i.e., the guard cells developing directly from an otherwise undifferentiated protodermal cell), but this hypothesis does not seem to require that any or all structurally distinct subsidiary cells be derived mesogenously.) There appears to be no reason why stomatal ontogeny could not vary in a species. Indeed, variation in mature stomatal morphology in individual leaves of *Cistanthe* suggests that this may be the case.

c. Other epidermal cell features. The surface outline of ordinary epidermal cells in the leaf intercostal region in *Cistanthe* ranges from orthogonal and nearly isodiametric in surface view (Figs. 80, 86, 90, 92–94) to irregular in shape with sinuous radial walls (Figs. 81, 84, 85). The entire range of variation occurs in individuals of some taxa, e.g., in *C. picta* (Figs. 82, 83). As might be expected, ordinary epidermal cells toward or overlying the midrib tend to be more elongate and quadrangular, presumably reflecting the pattern established by the young, rapidly elongating leaf primordium.

Ordinary epidermal cells of some *Cistanthe* species are more or less dimorphic, with large cells interposed among the smaller cells associated (or intergrading) with subsidiary cells (Figs. 89, 90). In extreme cases, the large cells form epidermal alveolae or papillae, such as in a specimen referable to *Cistanthe longiscapa* (*Worth & Morrison 16184*, see Table 1, Figs. 86, 87) and in species of sect. *Calyptridium* (Table 2), including *C. rosea* (Fig. 93). The epidermis of *C. cymosa* (Fig. 88) also appears somewhat papillate. Alveoli and/or papillae have been reported previously in "*Calandrinia lamprosperma* I. M. Johnston" (aff. *Cistanthe grandiflora*; Hershkovitz, 1991a; Johnston, 1929; but see also Kelley, 1973), in sect. *Calyptridium* (Hinton, 1975), and in *C. cephalophora* (I. M. Johnston) Carolin ex Hershkovitz (Kelley, 1973). The presence of papillate/alveolate cells in species of sect. *Calyptridium* varies among individuals (Hinton, 1975; pers. obs.).

Discussion

1. Leaf morphology and the circumscription of *Cistanthe*

Table 4 outlines a syndrome of nine leaf traits that typify *Cistanthe* and summarizes the distribution of these features in this genus and elsewhere in Portulacaceae. Leaf morphological data and illustrations for species of *Lewisia* and *Calandrinia* are presented elsewhere (Hershkovitz, 1990a, in press b, in press c), and the data for the remaining Portulacaceae will be presented in future publications. The taxonomic circumscriptions used in Table 4 are based on those proposed by Carolin (1987, in press), except for *Cistanthe*, which follows the present paper, and for *Calandrinia*, which follows Hershkovitz (1990a, in press a).

As indicated in Table 4, most of the leaf traits typifying *Cistanthe* are not universally present in the genus, and all occur elsewhere in the family. Hence, none can be designated a priori as a synapomorphy diagnostic of the genus, nor can any of their evolutionary polarities in the genus be determined a priori. Table 4 also indicates, however, that no other genus of Portulacaceae possesses the entire *Cistanthe* leaf-trait syndrome. Moreover, many of the traits of *Cistanthe* are rare in the other genera in which they occur. Therefore, the leaf morphology of *Cistanthe* appears to corroborate other morphological evidence for the naturalness of the genus as circumscribed here (Hershkovitz, 1990a, 1991c). That no distinctions between sect. *Calyptridium* and the remainder of *Cistanthe* are discernable from Table 4 should not be overlooked. Leaf morphology provides no evidence in support of Carolin's (1987, in press) retention of sect. *Calyptridium* as a distinct genus.

2. Leaf morphology and the relationship of *Cistanthe* to other Portulacaceae

Leaves of *Cistanthe* share features with various taxa throughout Portulacaceae (compare Table 4 and Fig. 2). The greatest degree of similarity appears to exist between *Cistanthe* and species of the Australian genus *Rumicastrum*. The absence

TABLE 4. Leaf traits of *Cistanthe*. Listed below are several leaf traits that occur commonly to universally among species of *Cistanthe*, their distribution in the genus, and their distribution elsewhere among Portulacaceae (Hershkovitz, 1991c, in press a, in press b, in press c, unpublished).

Trait	Distribution in *Cistanthe*	Distribution elsewhere among Portulacaceae
Winged petiole differentiated from blade	Rarely absent in broader-leaved species	Common in Montieae and *Calandrinia* sects. *Calandrinia* and *Monocosmia*; rare in *Lewisia* spp.; in one *Rumicastrum* sp.
Leaf base broad, nearly or quite clasping	All species	Montieae, *Calandrinia*, *Lewisia*, *Lenzia*; otherwise apparently absent
Festooned brochidodromous venation pattern	All species except those in which the leaves are extremely small and/or narrow	Weakly evident in broader-leaved *Talinum* spp., *Ceraria* spp., and *Portulaca* spp.; rarely and weakly evident in *Lewisia* spp.; *Talinella*
Primary vein weak to obsolete at leaf apex	Weak to obsolete in all species	Weak but usually evident in *Rumicastrum* and *Talinopsis*; weak to obsolete in *Portulacaria*, *Talinaria*, *Ceraria* spp., *Portulaca* spp., and *Calandrinia* sect. *Calandrinia* spp.
4° veins distinct	Distinct in several larger-leaved species throughout the genus, absent in smaller- and narrower-leaved species	Evident in broader leaves of *Ceraria* spp.; rarely distinct in *Portulaca*, as in *P. lutea*; weakly evident in broad leaves of *Claytonia megarhiza*, broader-leaved *Lewisia* spp., *Calandrinia* sects. *Acaules* and *Calandrinia* spp., and *Talinum* sect. *Talinum* spp.
Sinuous veins	In nearly all examined species except *C. tweedyi*, but hardly evident in the *C. umbellata* complex and individuals of the *C. picta* complex	Evident in some *Ceraria* spp., *Talinum* spp., and *Rumicastrum* spp.
Ribbonlike veins	Distribution same as sinuous veins	Present in (all?) species of *Talinum* sect. *Phemeranthus* but not common nor well-developed in *Talinum* sect. *Talinum*; in many, but not all *Rumicastrum* spp.; and in *Talinopsis* and *Grahamia*
Predominance of brachyparacytic stomata (incl. hemi-, amphi-, and "hemi"-amphivariants, see Fig. 95)	Characteristic of nearly all species	Characteristic of many Montieae spp.; *Calandrinia* sects. *Dianthoideae*, *Hirsutae*, and a few *Acaules* spp.; *Lenzia*; stems of *Talinum* sect. *Talinum* spp. but probably not leaves; rare in *Lewisia* spp. and *Rumicastrum* spp. (see also Nyanyano, 1986b)
Contact cells mostly 4, otherwise mostly 5, rarely 3 or 6, probably never 2 or more than 6	In all species	In all examined Montieae, *Calandrinia* and *Lenzia* spp.; in at least two *Rumicastrum* and one *Lewisia* spp.; otherwise probably rare in these genera; in *Talinum* sect. *Talinum* stems, but probably not leaves

of both festooned brochidodromous venation and strongly differentiated higher vein orders in *Rumicastrum* species is not surprising because their leaves are usually small and/or relatively narrow. Most species of *Rumicastrum* have a type of three-dimensional venation not evident in *Cistanthe* (Hershkovitz, unpublished), but the planar venation patterns in other species are hardly distinct from

those in the very narrow-leaved species of *Cistanthe*. The phylogenetic significance of this similarity remains to be determined.

The large number of shared leaf traits for *Cistanthe* and *Rumicastrum* indicated in Table 4 may be misleading because some traits typical of the former occur only rarely in the latter and not in combination with other traits. For example, the petiolar morphology characteristic of many species of *Cistanthe* occurs only in *Rumicastrum pumila* (F. Muell.) ined. (≡ *Calandrinia pumila* F. Muell.). This species is also similar to typical *Cistanthe* in its stomatal morphology, but it lacks ribbonlike veins and has a primary vein that is prominently dilated at the leaf apex. Moreover, this species has pantoporate-operculate pollen, which is regarded in terms of aperture number and morphology as derived in *Rumicastrum* (Kelley, 1973; Carolin, 1987; Hershkovitz, 1990a, in press a). Otherwise, I have found *Cistanthe*-like stomatal morphology only in *Rumicastrum remota* (I. M. Black) ined. (≡ *Calandrinia remota* I. M. Black), a species with 12–15-pantocolpate pollen, which is the putatively primitive condition in *Rumicastrum* (Kelley, 1973; Hershkovitz, 1990a, in press a; but see also Carolin, 1987). *Rumicastrum remota* has a three-dimensional venation pattern typical of many species of *Rumicastrum* and unlike three-dimensional venation in any species of *Cistanthe*. Other species of *Rumicastrum* possess various stomatal types having three, rather than four or five, contact cells; e.g., anisocytic (Hershkovitz, unpublished).

Leaves of *Cistanthe* are mostly less similar to those of other genera of Portulacaceae than to those of *Rumicastrum*. With respect to their leaf morphological similarity to *Cistanthe*, most Portulacaceae fall into one of two categories: (1) those taxa having in common with *Cistanthe* characters of gross and epidermal morphology, e.g., Montieae, *Calandrinia*, and *Lewisia*; and (2) those taxa having in common with *Cistanthe* venation features, e.g., *Talinum*, *Ceraria*, and others listed in Table 4. These two groups are otherwise potentially distinct cladistically (see Fig. 2), as well as biogeographically: the first group, along with *Cistanthe*, comprises the genera of Portulacaceae that occur predominantly westward from the American cordillera, and the second group comprises most of the taxa that occur predominantly eastward from the American cordillera and in southern Africa (Hershkovitz, 1990a–c, in prep.). Thus, while the leaf data presented here do not resolve the phylogenetic position of *Cistanthe*, they seem to suggest a pivotal position of this genus in Portulacaceae, potentially linking the eastern American/African, western American, and Australian members of the family.

3. LEAF MORPHOLOGY AND RELATIONSHIPS WITHIN *CISTANTHE*

Leaf morphology appears to have limited utility for diagnosing or assessing relationships among the sections of *Cistanthe*. Sections of *Cistanthe* are not distinguishable on the basis of leaf features, although, as noted, the monotypic sect. *Strophiolum* lacks sinuous veins and ribbonlike veins. Distinctions in venation pattern and epidermal morphology are not evident among Reiche's (1897, 1898) subdivisions of *Cistanthe* sect. *Cistanthe* (i.e., *Calandrinia* sects. *Cistanthe*, *Rosulatae*, *Arenariae*, and *Andinae*), except to the degree that Reiche's circumscriptions of *Calandrinia* sects. *Cistanthe* and *Andinae* consist of the *Cistanthe grandiflora* and *Cistanthe picta* species complexes, respectively (Hershkovitz, 1991a). Kelley's (1973) assignments of the extra-Chilean species of *Cistanthe* to Reiche's (1897, 1898) sections of *Calandrinia* cannot be independently corroborated by venation and epidermal evidence. The monophyly of *Cistanthe* sect. *Calyptridium* might be evidenced by the pervasiveness of sunken stomata and leaf surface papillae (see Table 3), but both traits occur elsewhere in the genus. Likewise, the absence of sinuous and ribbonlike veins in *Cistanthe* sect. *Strophiolum* is not unique to this taxon. Nevertheless, the sectional status of sect. *Strophiolum* is recognized partially on the basis of these traits (Hershkovitz, 1990a, in press c).

The utility of leaf morphology in elucidating species-level phylogeny in *Cistanthe* is limited to the degree that the variable characters show constancy in otherwise diagnosable taxa and are polarizable. The utility is, therefore, inherently restricted given the poorly defined species limits in *Cistanthe* and uncertainty regarding outgroups of the genus (Hershkovitz, 1990a, 1991a). Reiche (1897) emphasized gross leaf morphology in his keys to the Chilean species of *Cistanthe*, but the apparent high degree of plasticity and continuous range of variation in gross leaf morphology as observed here contribute to the inadequacy of Reiche's keys for identifying the Chilean material. The results presented above, however, provide at least some evidence that species or species complexes (e.g., *Cistanthe grandiflora*, *C. picta*, *C. umbellata*) can be distinguished by their combined leaf traits. It is possible, therefore, that multivariate morphometric analyses of leaf morphological pa-

TABLE 5. Leaf traits having a restricted occurrence in *Cistanthe*. Listed below are leaf traits rare in *Cistanthe*, their distribution in the genus (see text), and their distribution elsewhere among Portulacaceae (Hershkovitz, in press 1991c, in press a, in press b, in press c, unpublished).

Trait	Distribution in *Cistanthe*	Distribution elsewhere among Portulacaceae
Leaves over 3,000 mm²	*C. grandiflora* complex, *C. paniculata* complex, and *C. tweedyi*	*Talinum* sect. *Talinum*, *Lewisia congdonii*, *L. cotyledon*, and *Claytonia* spp.
Fifth-order veins distinct	*C. umbellata* complex; weakly evident in *C. longiscapa* and *C. paniculata*	Absent
Three-dimensional venation	*C. grandiflora* complex, *C. paniculata* complex, and *C. ambigua*	*Talinum* sect. *Phemeranthus*, nearly all *Portulaca* sect. *Portulaca*, *Talinopsis*, *Grahamia*, *Schreiteria*, *Lewisia rediviva*; some, but not all *Anacampseros* spp. and *Rumicastrum* spp.
Large proportion of anomocytic stomata	*C. quadripetala*	*Lewisia triphylla*, *L. kelloggii*, and *Montia* spp. (see also Nyanyano, 1986a, b)
Papillae/alveoli on leaf surface	Variably present in sect. *Calyptridium* and specimens of sect. *Cistanthe* (see text)	*Anacampseros* spp., one species of *Calandrinia* sect. *Acaules*, one species of *Rumicastrum*
Amplexicaul leaves	Specimens of *C. paniculata* complex (see text)	*Claytonia* spp., but probably not homologous (see text)

rameters may help refine ideas on species limits in *Cistanthe*.

A few leaf traits in certain species of *Cistanthe* are possibly or likely derived in the genus (Table 5): (1) leaves larger than 3,000 mm²; (2) fifth-order leaf venation; (3) three-dimensional leaf venation; (4) a large proportion of anomocytic stomata; (5) papillate or alveolate cells throughout the leaf surface; and (6) amplexicaul leaves. There is no compelling structural or phylogenetic evidence that these traits are symplesiomorphic with similar traits in other Portulacaceae. The leaf-size character is most troublesome, because leaf size varies in all taxa and, presumably, is influenced by environmental factors. The size of the largest leaves in *Cistanthe*, however, exceeds that found in all but a few scattered taxa in the family. The relatively strong differentiation of higher vein orders found in a few species of *Cistanthe* is almost certainly derived because this trait is absent elsewhere in the family. Three-dimensional venation is a complex characteristic because more than one manifestation is present in *Cistanthe* and in other Portulacaceae. In at least some cases, other members of Portulacaceae with three-dimensional venation seem to be most closely related to species with planar venation. For example, in *Portulaca*, three-dimensional venation is restricted to *P.* sect. *Portulaca* (Hershkovitz, unpublished). This section is thought to be derived in the genus (Geesink, 1969, 1987). Therefore, three-dimensional venation has probably evolved several times in the family. In *Cistanthe*, anomocytic stomata are common only in a species of sect. *Calyptridium*. This section is probably relatively derived in the genus (Hershkovitz, 1990a, 1991c). The leaf surface papillae/alveoli that occur in *Cistanthe* appear to be very large cells that protrude beyond the smaller epidermal cells; those in *Anacampseros* and *Calandrinia* sect. *Acaules* are more hairlike, and those in the latter are also ribbed (Hershkovitz, 1990a, in press b). Unribbed papillae have been reported in *Rumicastrum quadrivalvis* (F. Muell.) ined. (≡ *Calandrinia quadrivalvis* F. Muell.; cf. Kelley, 1973) but the specimen was not vouchered and other specimens of *R. quadrivalvis* lack papillae (Hershkovitz, 1990a, in press b). The amplexicaul leaves that occur in *C. paniculata* are not homologous with superficially similar "perfoliate" leaves in species of *Claytonia*, which are formed by the congenital fusion of two leaves at a node.

Because the characters listed in Table 5 are mostly restricted to recognized species or species complexes, they provide little insight into the phylogeny of *Cistanthe*. For example, epidermal papillae/alveoli may represent a synapomorphy of sect. *Calyptridium*, but these species are presumably closely related in any case (Hershkovitz, 1990a,

1991c; Hinton, 1975). An especially close relationship between papillate-leaved species in sect. *Calyptridium* and sect. *Cistanthe* is not supported by additional characters. Large leaves and similar three-dimensional venation may be indicative of relationship between the *C. grandiflora* and *C. paniculata* complexes. These species complexes occupy adjacent desert habitats in northern Chile and southern Peru, respectively. Both possess long-haired seeds, which are otherwise of restricted occurrence in *Cistanthe* (Kelley, 1973), although glabrous seeds also occur in both complexes (Hershkovitz, 1990a, 1991a; Johnston, 1929). Otherwise, leaves of *C. paniculata* (Figs. 3, 22, 39), which have very wide, obovate laminae and relatively well developed vein orders, more closely resemble leaves of the northern Chilean *C. longiscapa* complex (Figs. 4, 23, 40; cf. Figs. 8, 9, 27, 44), in which long-haired seeds also occur (Hershkovitz, 1990a, 1991a). Kelley (1973) assigned *Cistanthe paniculata* to *Calandrinia* sect. *Cistanthe* Reiche, which includes the *Cistanthe grandiflora* complex (Reiche, 1898), whereas Reiche (1898) assigned *Cistanthe longiscapa* to the highly variable *Calandrinia* sect. *Rosulatae* Reiche.

4. LEAF FORM, FUNCTION, AND EVOLUTION IN *CISTANTHE*

While the aim of this survey of leaf morphological diversity in *Cistanthe* was to help resolve phylogenetic and taxonomic questions, the data pose questions on the relationship of leaf form to function and evolution. Such questions cannot be answered from a survey of herbarium specimens alone, but preliminary data such as that generated here might provide a focus for future ecophysiological and evolutionary investigations. Only a few aspects of leaf form that have been studied with respect to function will be considered in the data presented here for *Cistanthe*, including gross leaf morphology, leaf venation pattern, sinuous and ribbonlike veins, and subsidiary cell morphology.

Givnish (1979, 1982, 1984) has developed several models that relate aspects of leaf form (e.g., leaf shape, arrangement, venation pattern) to the optimization of photosynthetic ability and the minimization of the metabolic cost of leaf support and supply. Givnish (1979) suggested rosette-forming herbs might be expected to have obovate leaves that, collectively, form a circular photosynthetic area that mimics an optimally efficient light-capturing structure. *Cistanthe* species have predominantly basal and/or suprabasal leaves and usually have relatively few cauline leaves except in species that form secondary rosettes along prostrate branches. The leaves are, in accordance with Givnish's model, typically obovate to oblanceolate (see above). In the *Cistanthe picta* complex, which has more diffusely arranged cauline leaves (Hershkovitz, 1991a; Reiche, 1898), the basal leaves are sessile and oblanceolate to obovate while the cauline leaves tend to be more petiolate with orbicular to ovate blades. The morphology of the cauline leaves might be explained with reference to Givnish's (1979) stem-leaf packing model, which purports that stem-leaf bases are evolutionarily honed to eliminate the portion that would be shaded by other leaves. Departures from the predicted form of *Cistanthe* leaves (e.g., linear leaves or petiolate leaves with a small, distal, rhombic blade portion, as in the *Cistanthe arenaria* complex; Hershkovitz, 1991a; Reiche, 1898) might best be explained as adaptations to xeric conditions, in which the leaf area is reduced to resist overheating and reduce water loss.

Givnish (1979) also noted that obovate leaves of rosette-forming plants, which are supported by the ground, or especially thick cauline leaves, which are supported independently of the vascular tissue, may tend to evolve parallel venation in order to maximize the efficiency of water and nutrient supply. He supposed that the pinnate venation pattern typical of dicotyledons provides an optimal support system (but a suboptimal supply system) for the cantileverlike form of cauline leaves. Superficially, it would appear that leaves of *Cistanthe* are supported primarily by their thickness and broad, clasping leaf bases, or, in the case of rosette leaves, by other leaves and/or the ground. The primary vein in *Cistanthe* does not seem to be well-suited for support because of its irregular, zig-zag, or sinuous course and its relatively small size in the broader portion of the leaf blade. Yet venation in *Cistanthe* is basically pinnate, although the secondary veins may arise at a particularly narrow angle (e.g., in *C. guadalupensis*, Fig. 5, a species with all basal leaves; Hershkovitz, in press c; Rydberg, 1932). Thus, the pinnate venation patterns of *Cistanthe* appear to represent an exception to Givnish's (1979) model.

The functional significance of the peculiar ribbonlike veins of *Cistanthe* is difficult to evaluate without more detailed anatomical and developmental data. In the vascular bundles of primary stem tissue, the centrifugally developing sequence from protoxylem elements with annular thickenings to metaxylem elements with scalariform thickenings is thought to facilitate vascular supply during the course of stem elongation and maturation. A

similar function might be suspected for ribbonlike veins if the succulent leaves continue to grow for a prolonged period after becoming functional. Whether the sinuousness of the veins serves any function cannot be evaluated without prior determination that this is not a preparatory artifact. The sinuousness might reflect the ability of the leaf to expand and contract under oscillating water regimes.

The functional significance of subsidiary cell shapes and arrangements does not appear to have been extensively studied. Reviews of stomatal function and cell biology (e.g., Sack, 1987; Salisbury & Ross, 1985) tend to emphasize the structure and physiology of the guard cells, while reviews of stomatal supracellular morphology (e.g., Wilkinson, 1979) emphasize gross form and development. Payne's (1979) brief review of stomatal morphology is unusual in considering both.

Reviews of stomatal function emphasize that guard cells are protoplasmically isolated from other leaf cells (Sack, 1987), and that the "surrounding cells" (≡ contact cells) serve as a source of potassium ions that are transported into guard cells and affect stomatal opening (Salisbury & Ross, 1985). The morphology and spatial distribution of the contact cells undoubtedly influence this physiological process (Payne, 1979; Salisbury & Ross, 1985: 62, figs. 3–9), but whether extreme differences in stomatal complex morphology (e.g., in hexacytic vs. anomocytic stomata) have any net effect on this process is not clear. Payne (1979) observed a correlation between mesogenous stomatal development (presumably resulting in guard cells surrounded by distinct subsidiary cells) and the ability of the plant to withstand water stress, e.g., in succulent leaves. Leaves of *Cistanthe* are unquestionably succulent and presumably dry-adapted, yet mesogenous stomatal development does not appear to be the rule, or perhaps even especially common, in the genus (see above). In any case, *Cistanthe* (and/or other Portulacaceae in which marked differences in stomatal morphology occur in closely related taxa; Hershkovitz, in press b, in press c), might provide a natural system for investigating subsidiary cell/guard cell physiological interactions.

The development of the stomatal complex has been studied extensively among angiosperms, but as with physiology, the functional significance of the various ontogenetic pathways is apparently poorly understood. Payne (1979) proposed a sort of "tailoring" function for subsidiary cells; i.e., their development compensates for the difference in cell enlargement between ordinary epidermal and guard cells. This hypothesis seems plausible in instances where the perimeter of a stomatal complex (i.e., the guard and apparent subsidiary cells) conforms to the dimensions of the adjacent ordinary epidermal cells, e.g., in Figures 80 and 81. The hypothesis does not, however, explain the anomocytic condition (Fig. 91), in which the guard cells are directly adjacent to the much larger epidermal cells, or instances where the perimeter of the stomatal complex appears to have greater dimensions than those of the adjacent epidermal cells (e.g., Fig. 84).

The goal of understanding the functional or adaptational value of leaf morphological features renders an understanding of the taxonomy and phylogeny of the plants in question all the more important. The fact that the leaf traits of *Cistanthe* conform to simple functional models in some ways but not others indicates that additional factors, be they genetic or epigenetic, sometimes influence leaf morphology in the genus. The genetic factors, collectively, reflect evolutionary history. Correlations are evident between the leaf traits of *Cistanthe* and environmental or developmental factors, but one should not overlook the fact that the collection of leaf traits shared by most or all members of the genus seem to correlate best with the co-occurrence of functionally unrelated traits, e.g., unequal inflorescence bracts. In other words, the leaf morphology of *Cistanthe* correlates best with other evidence that members of the genus share a common ancestor. Collectively, leaf traits permit members of *Cistanthe* to be distinguished from other members of Portulacaceae, including those that occupy at least the same general geographic region, and probably more so from other angiosperms, including those that might superficially resemble members of *Cistanthe* and/or occupy the same habitat. Resolution of phylogenetic relationships within *Cistanthe* (and Portulacaceae in general) will help clarify which traits were inherited from a more remote ancestor and which evolved more recently as members of the genus came to occupy their present habitats.

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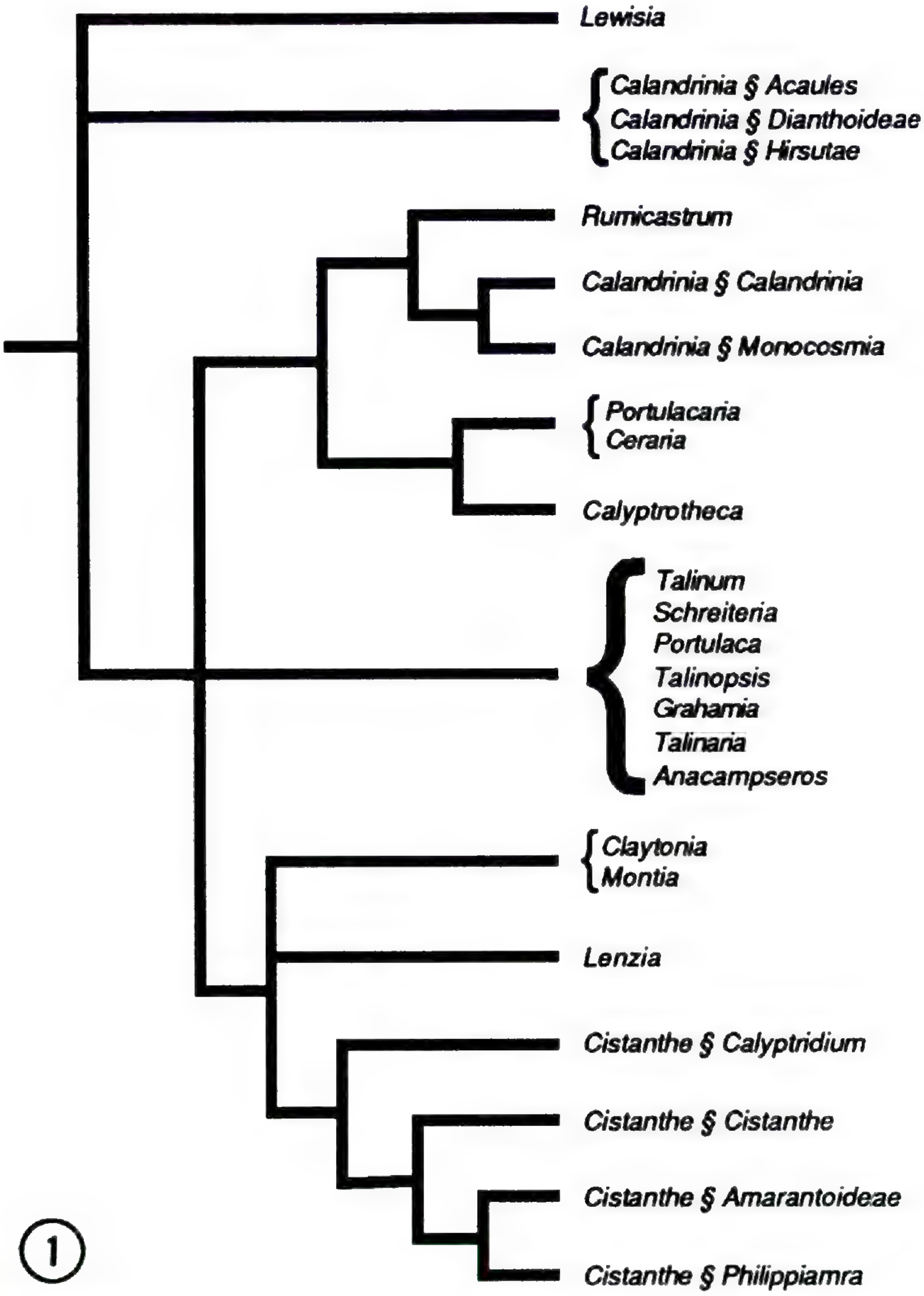

FIGURE 1. Simplified reproduction of Carolin's (1987: 402, fig. 7) most parsimonious cladogram of Portulacaceae, emphasizing the relationships among major clades and among members of *Cistanthe*. The taxonomy follows Carolin (1987, in press), except for *Cistanthe* and *Calandrinia*, which follows Hershkovitz (1990a, 1991c, in press a). The synapomorphies supporting the branching structure shown are problematic (see Hershkovitz, 1990a, 1991c).

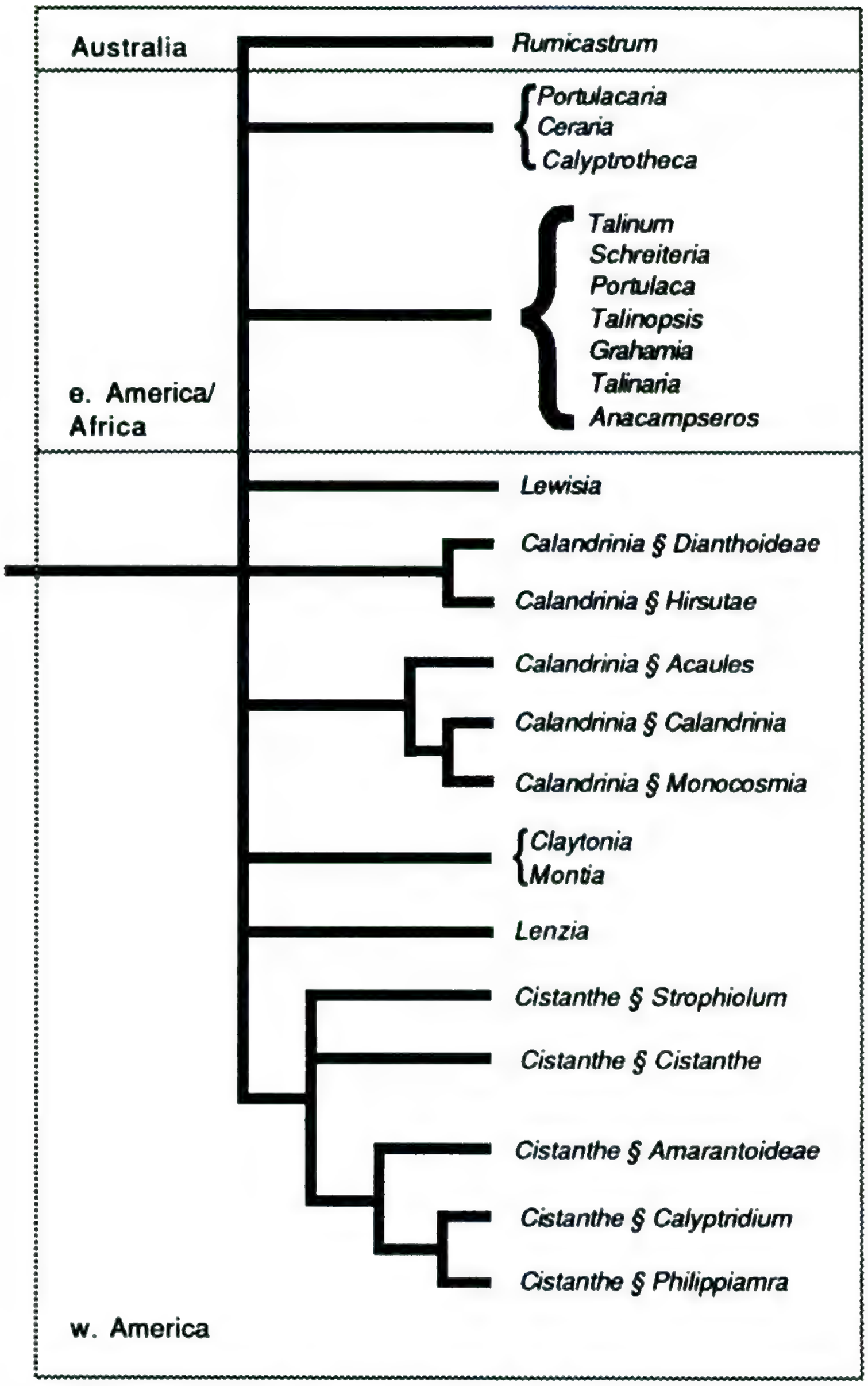

FIGURE 2. Revised cladogram of Portulacaceae emphasizing relationships among the sections of *Cistanthe* (see Hershkovitz, 1990a, 1991c) and showing relationships of *Calandrinia* sects. *Calandrinia* and *Monocosmia* I have proposed elsewhere (see Hershkovitz, 1990a, in press a). The taxonomy follows Carolin (1987, in press), except for *Cistanthe* and *Calandrinia*, which follows Hershkovitz (1990a, 1991c, in press a). The boxes enclosing portions of the diagram circumscribe the regions of endemism or greatest endemism of the included taxa (Carolin, 1987; Hershkovitz, 1990a, 1991c, in press a, in prep.).

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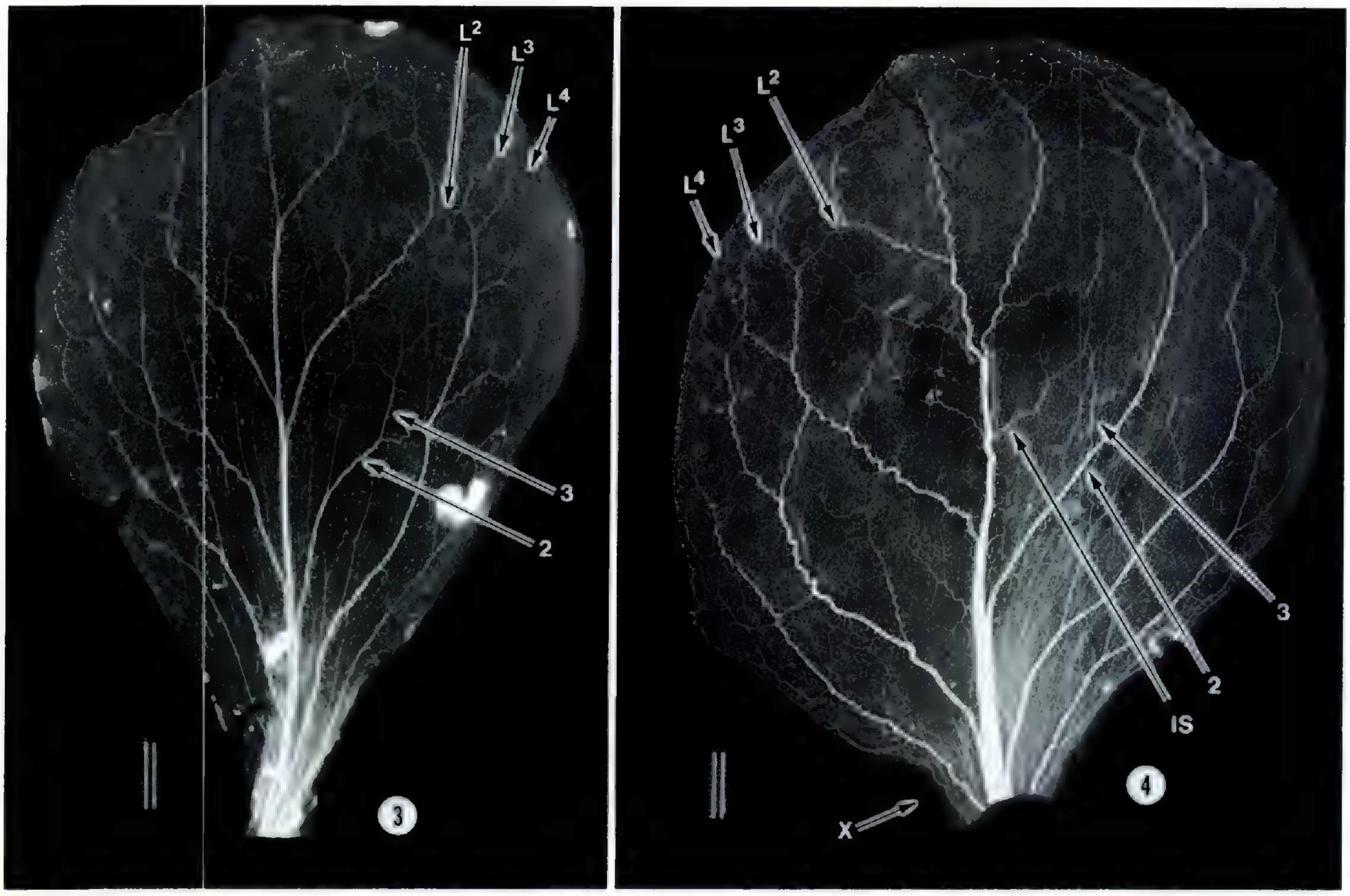
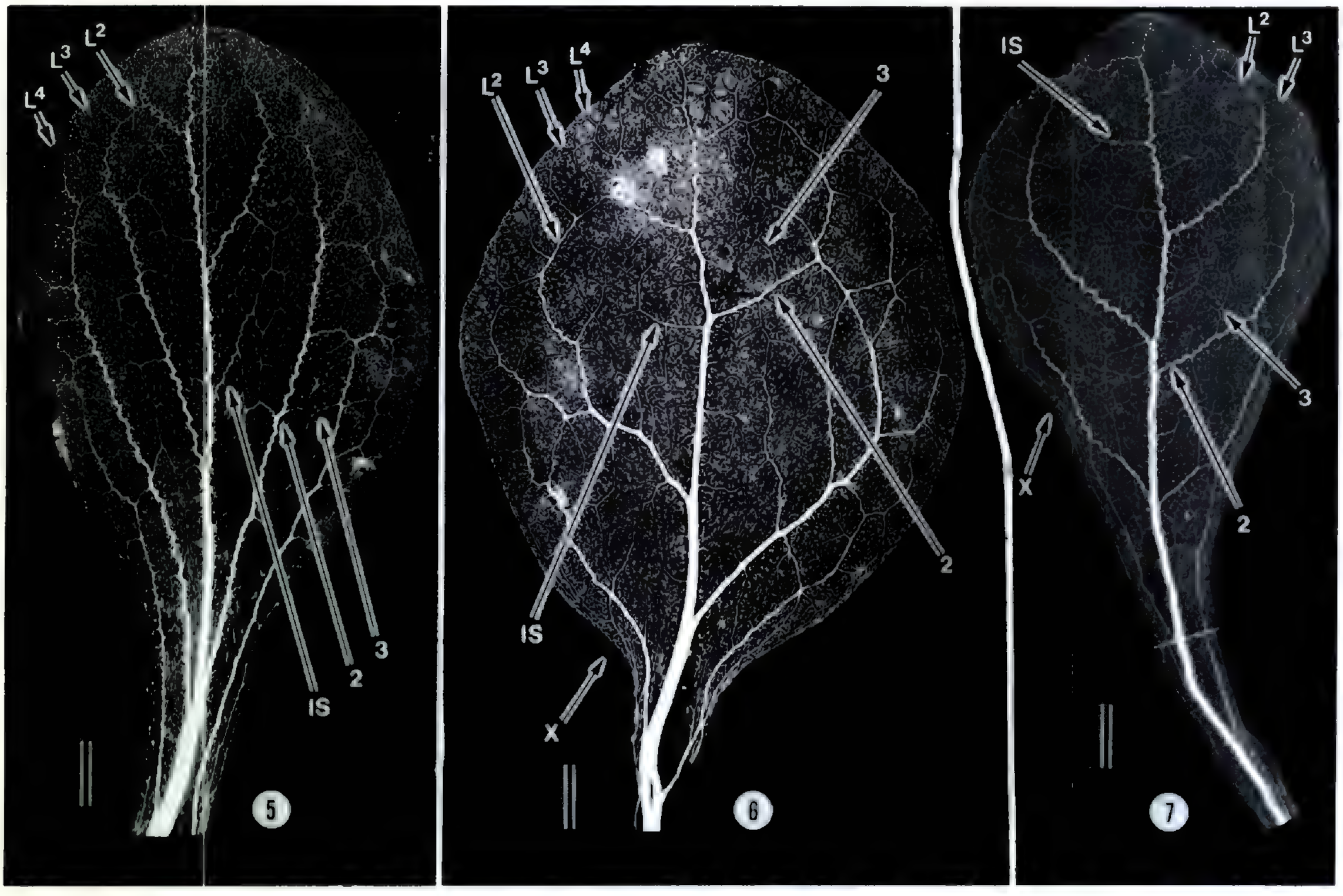
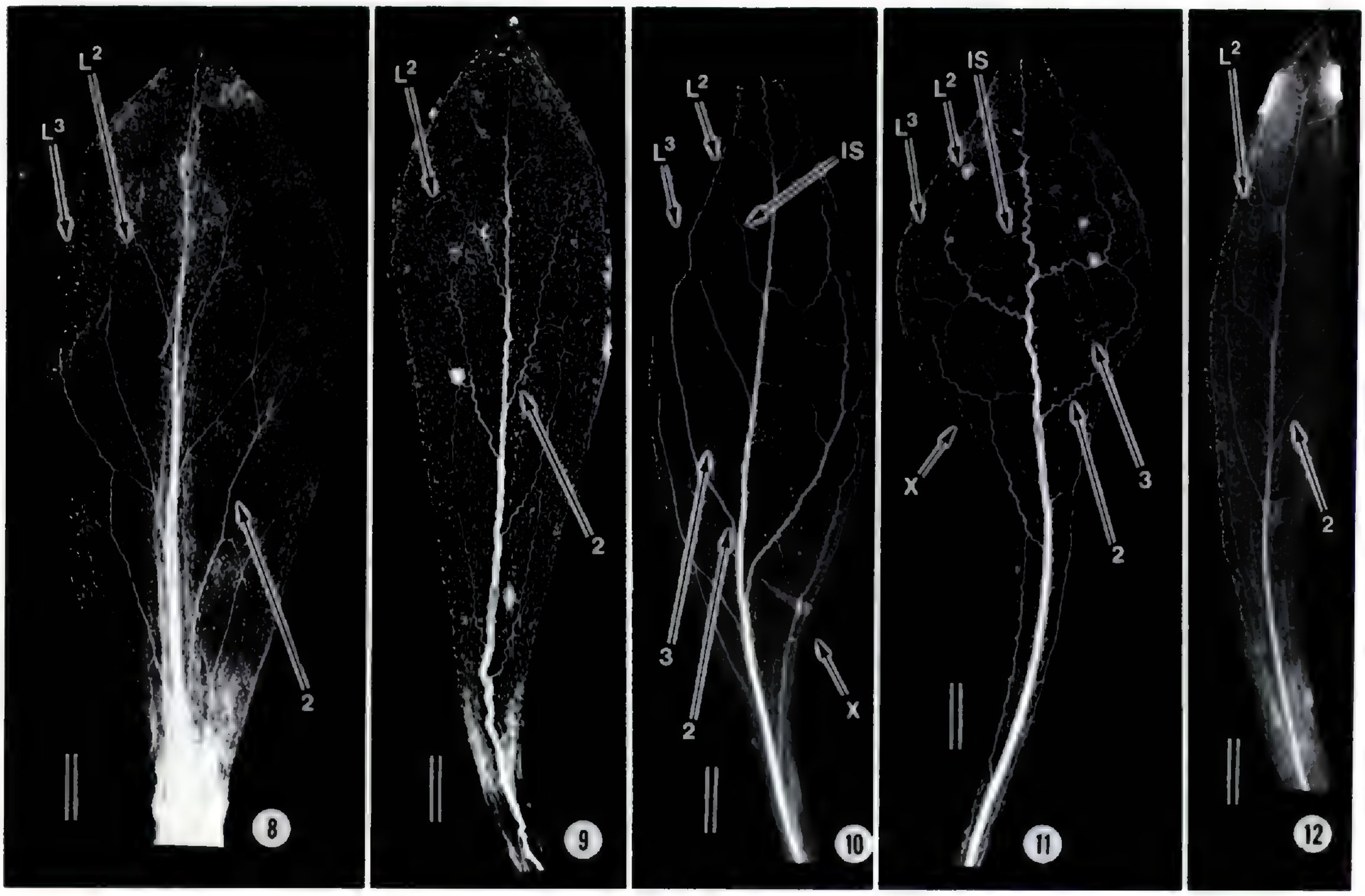
FIGURES 3–55. Gross venation features in *Cistanthe*. All vouchers are listed in Table 1. The specimens in Figs. 22–54 are the same as those in Figs. 3–21 and are not reidentified except where necessary. 1, primary vein, 2, secondary vein, etc.; L^2, secondary loop, L^3, tertiary loop, etc.; IS, intersecondary vein; X, the approximate position of the constriction between the blade and winged petiole.



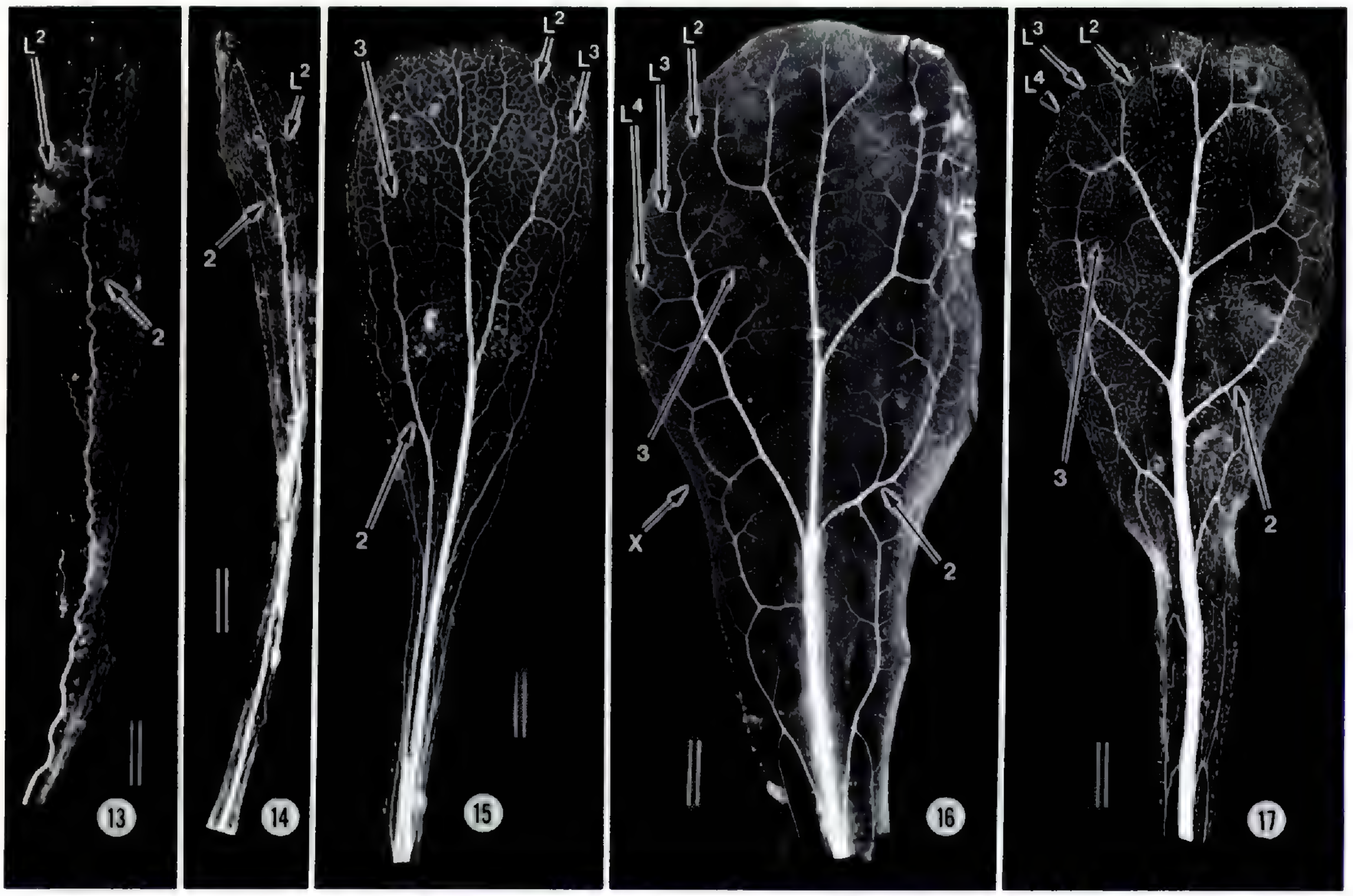
FIGURES 3, 4. Cleared whole leaves of *Cistanthe* sect. *Cistanthe*.—3. *C. paniculata* (*Ferreyra 12022*).—4. *C. longiscapa* (*Johnston 5034*). The petiole, ca. half as long as the blade, is not shown. Scale bars are (mm) ca. 6.2 and 3.0, respectively.



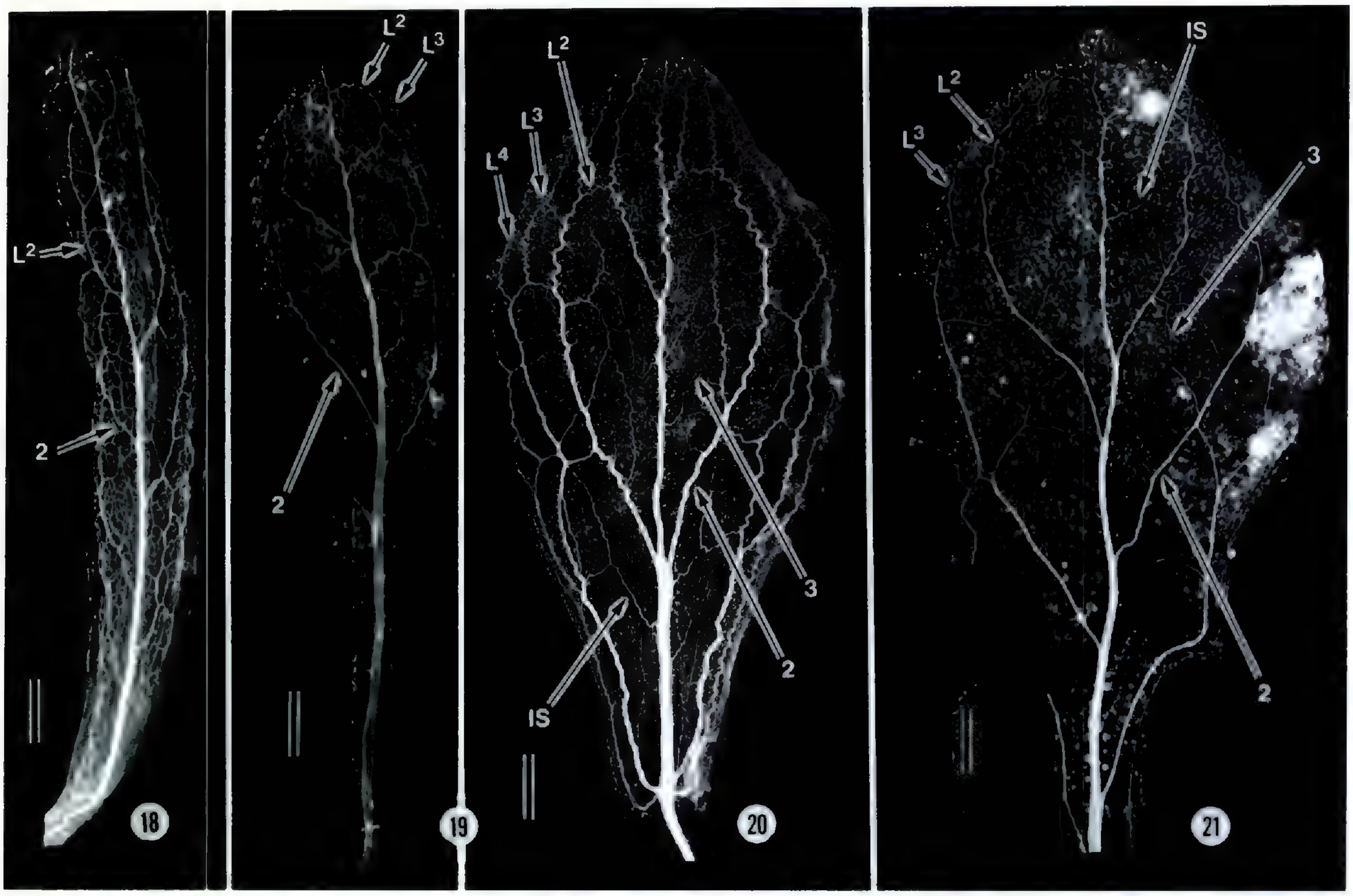
FIGURES 5–7. Cleared whole leaves of *Cistanthe* sect. *Cistanthe*.—5. *C. guadalupensis* (*Wiggins & Ernst 174*).—6. *C. picta* var. *picta* (*Kuntze s.n.*).—7. *C. coquimbensis* (*Werdermann 881*). Scale bars are (mm) ca. 4.6, 2.0, and 2.5, respectively.



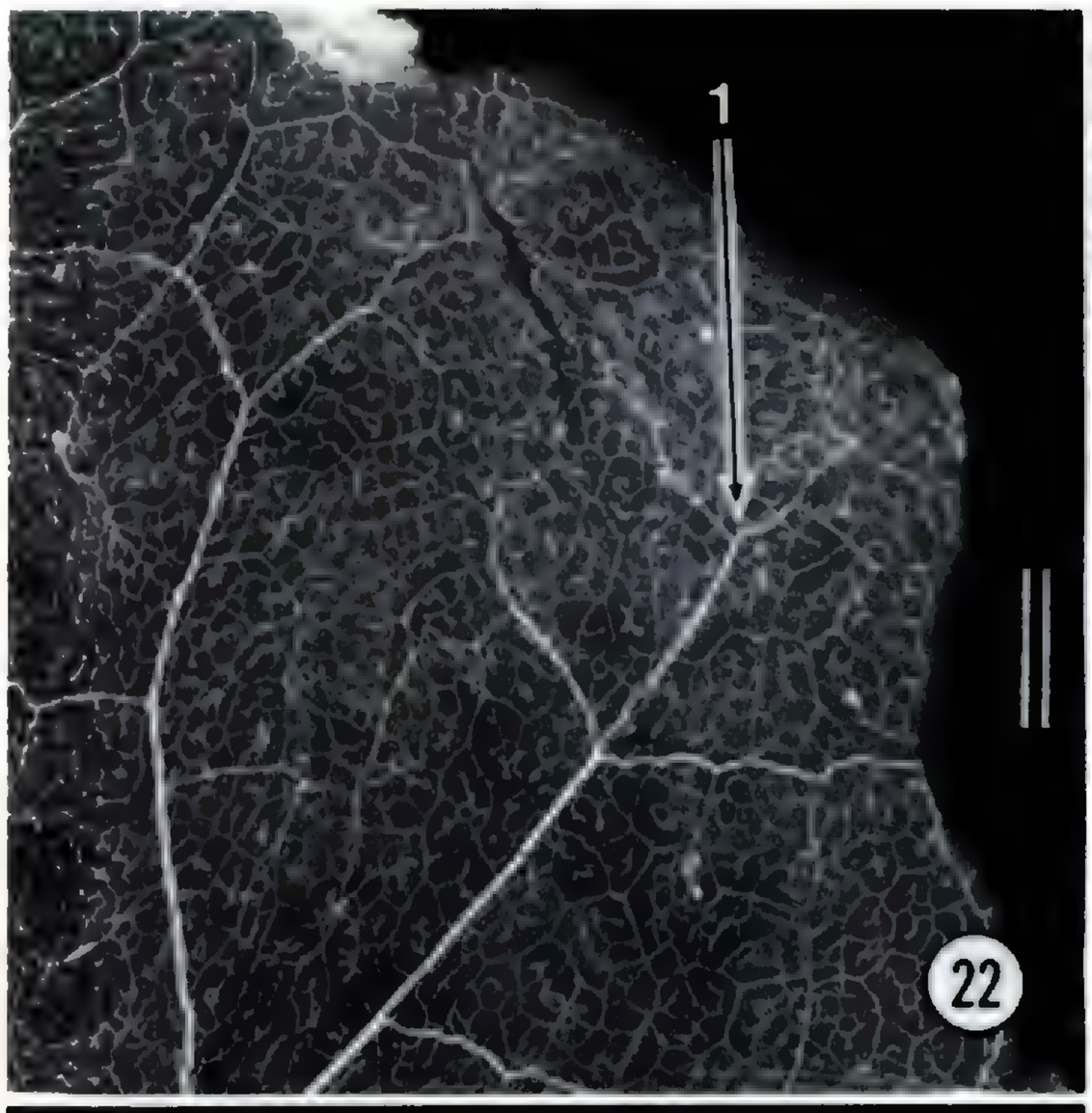
FIGURES 8–12. Cleared whole leaves of *Cistanthe* sect. *Cistanthe*.—8. *C. grandiflora* (*Werdermann 405*).—9. *C. grandiflora* (*Morrison et al. 16872*).—10. *C. weberbaueri* (*Weberbauer 5321*).—11. *C.* sp. cf. *arenaria* (*Zollner 10636*).—12. *C. lingulata* (*Lopez 374*). Scale bars are (mm) ca. 4.5, 2.8, 3.3, 3.0, and 2.1, respectively.

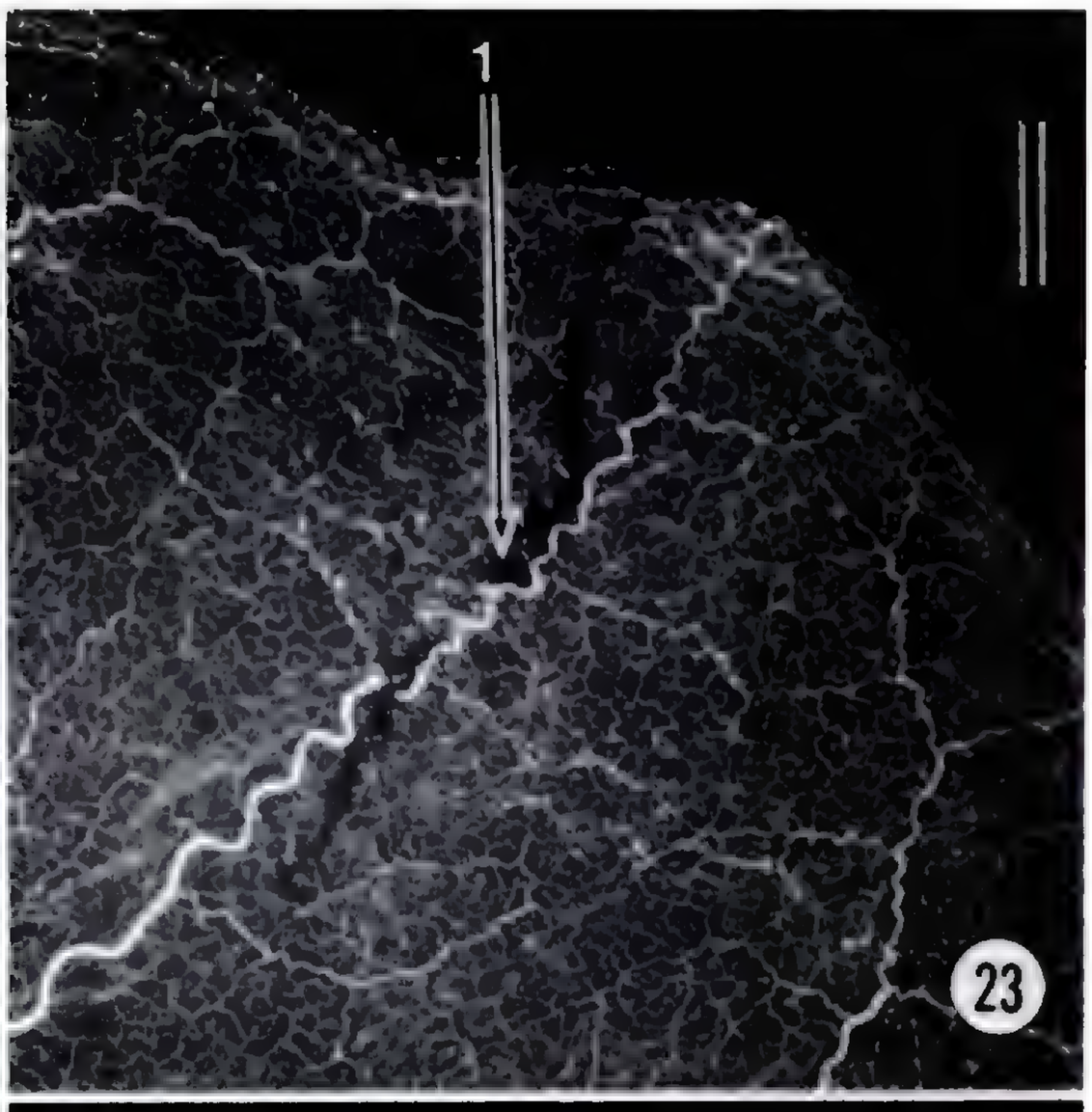


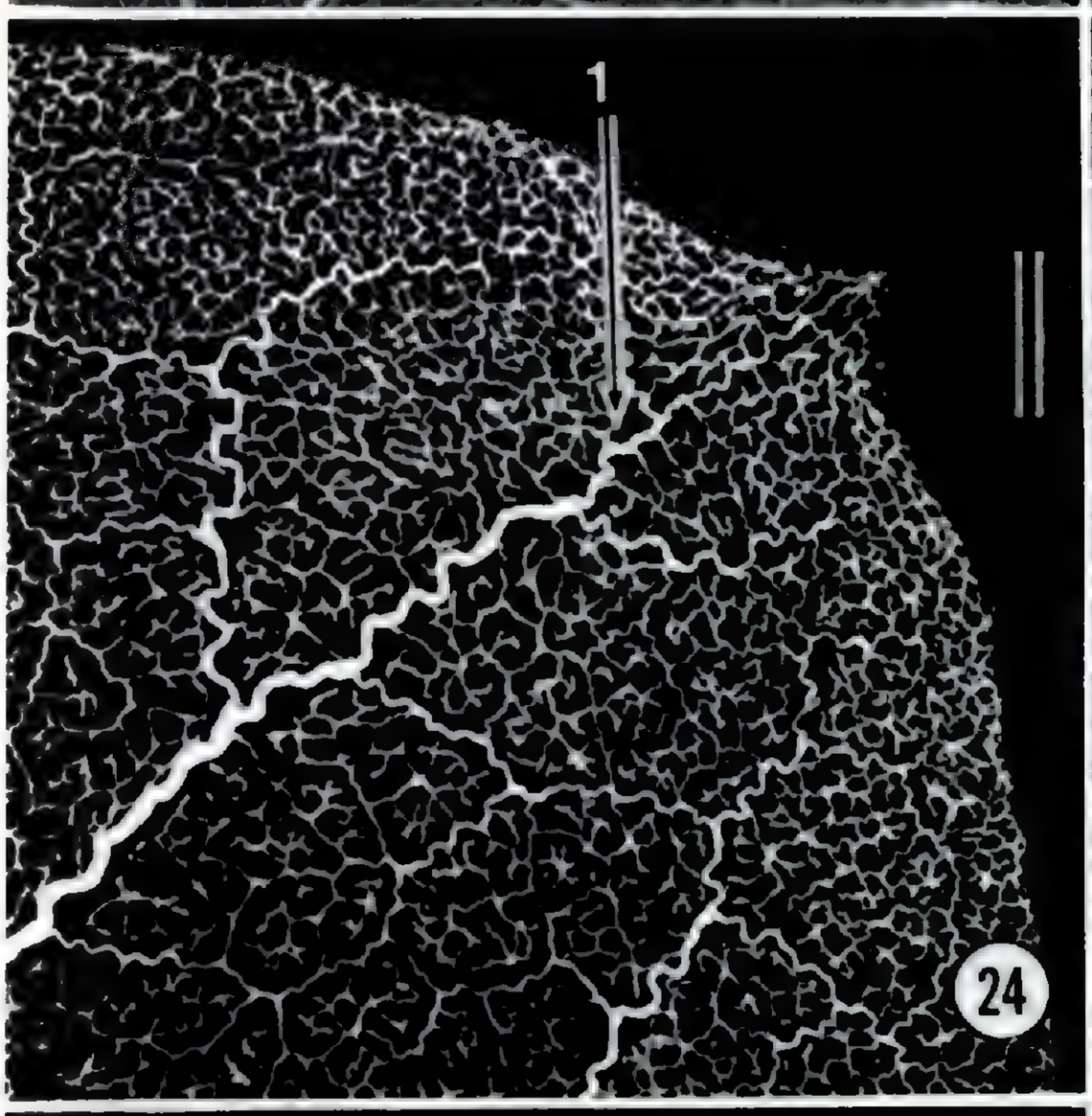
FIGURES 13–17. Cleared whole leaves of *Cistanthe* sects. *Cistanthe* (13, 14) and *Calyptridium* (15–17).—13. *C.* sp. (*Zollner 9807*).—14. *C. fenzlii* (*Philippi s.n.*).—15. *C. quadripetala* (*Hoover 3571*).—16. *C. monosperma* (*Heller 10804*). The petiole, ca. as long as the blade, is not shown.—17. *C. umbellata* (*Jones 2460*). Scale bars are (mm) ca. 2.8, 1.6, 3.4, 3.8, and 2.2, respectively.

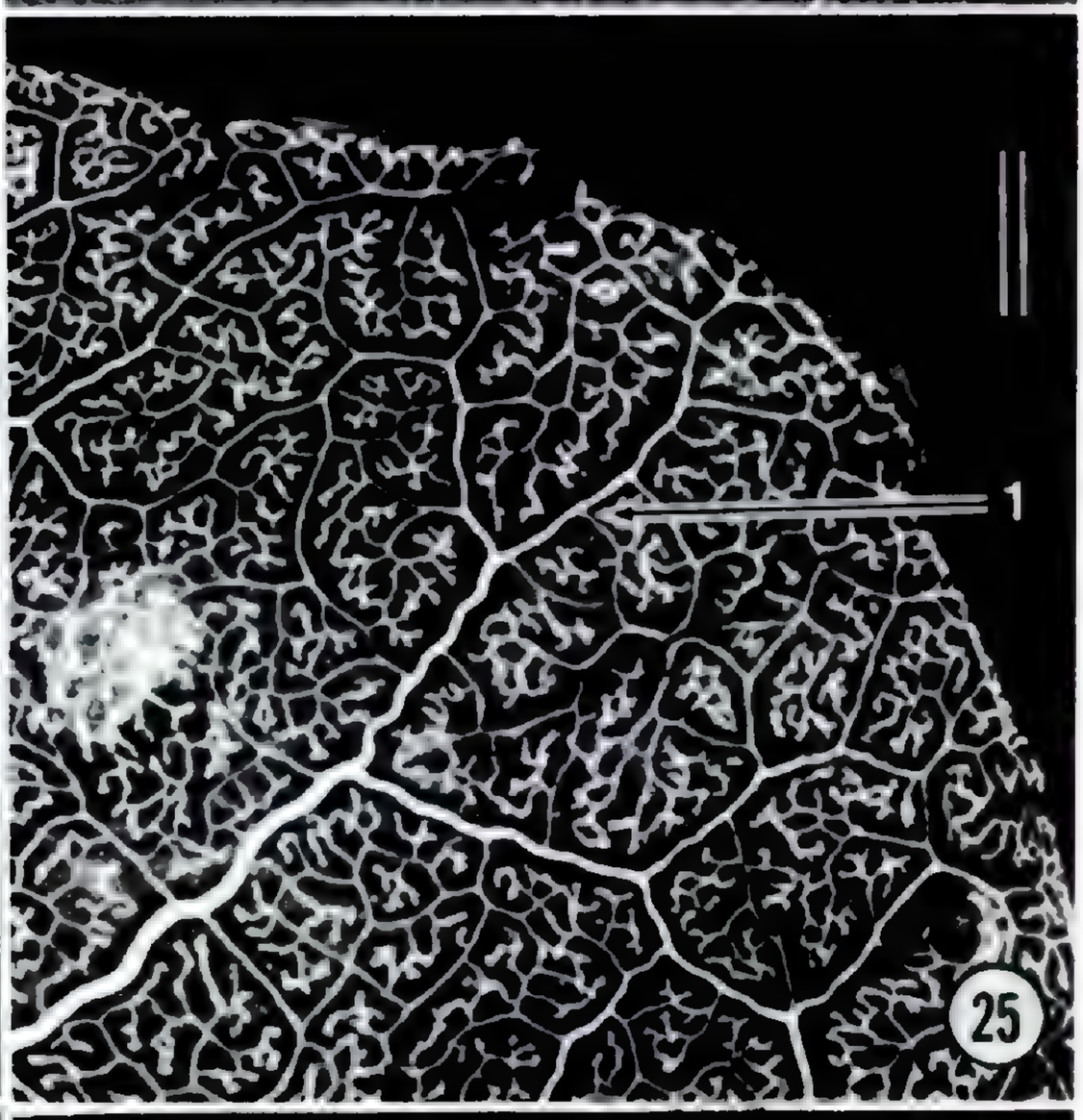


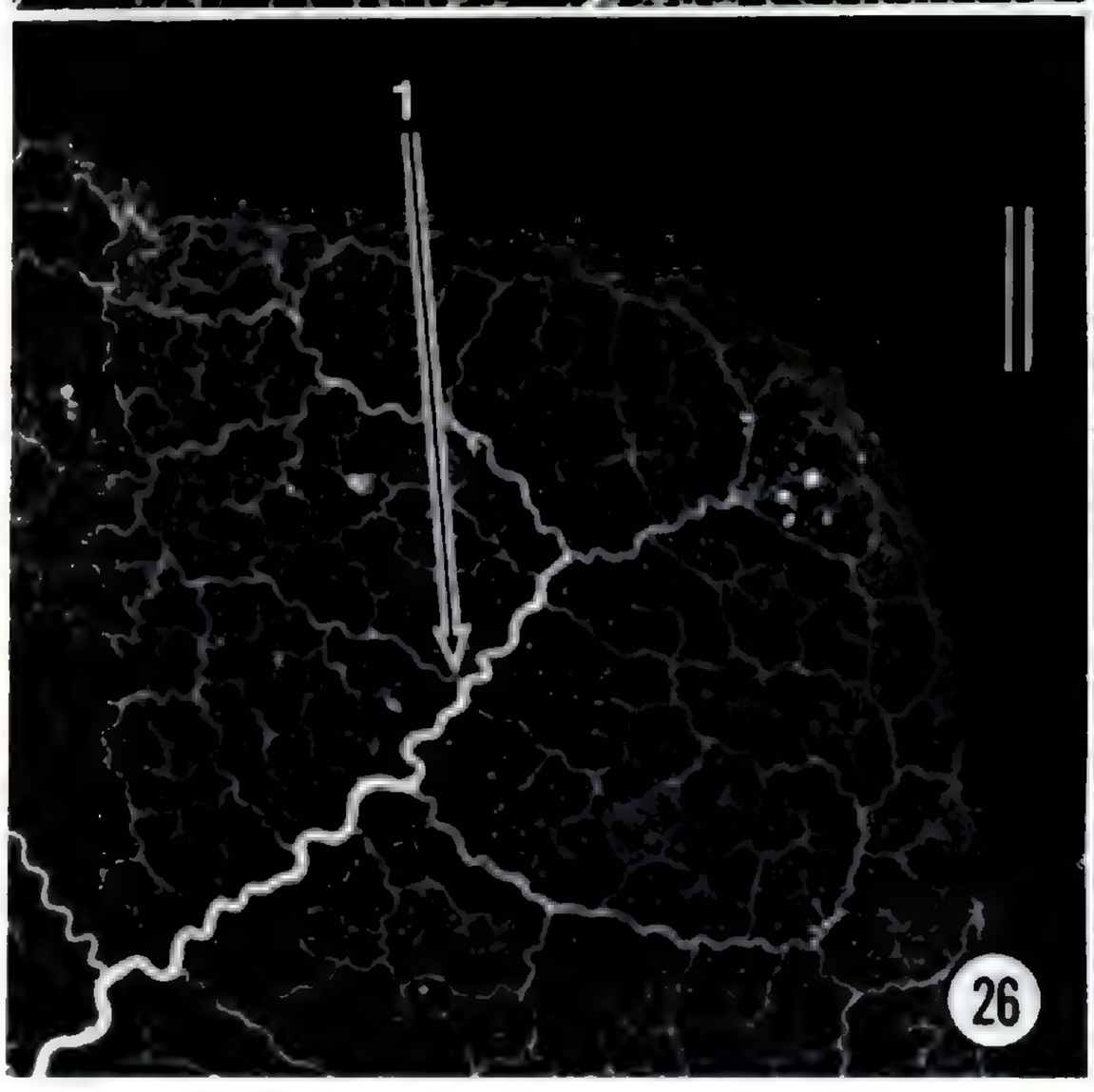
FIGURES 18–21. Cleared whole leaves of *Cistanthe* sects. *Amarantoideae* (18–20) and *Philippiamra* (21).—18. *C. ambigua* (*Nelson & Nelson 3287*).—19. *C. calycina* (*Johnston 5318*).—20. *C. salsoloides* (*Werdermann 1048*).—21. *C. celosioides* (*Worth & Morrison 15820*). Scale bars are (mm) ca. 3.0, 1.3, 2.4, and 1.5, respectively.

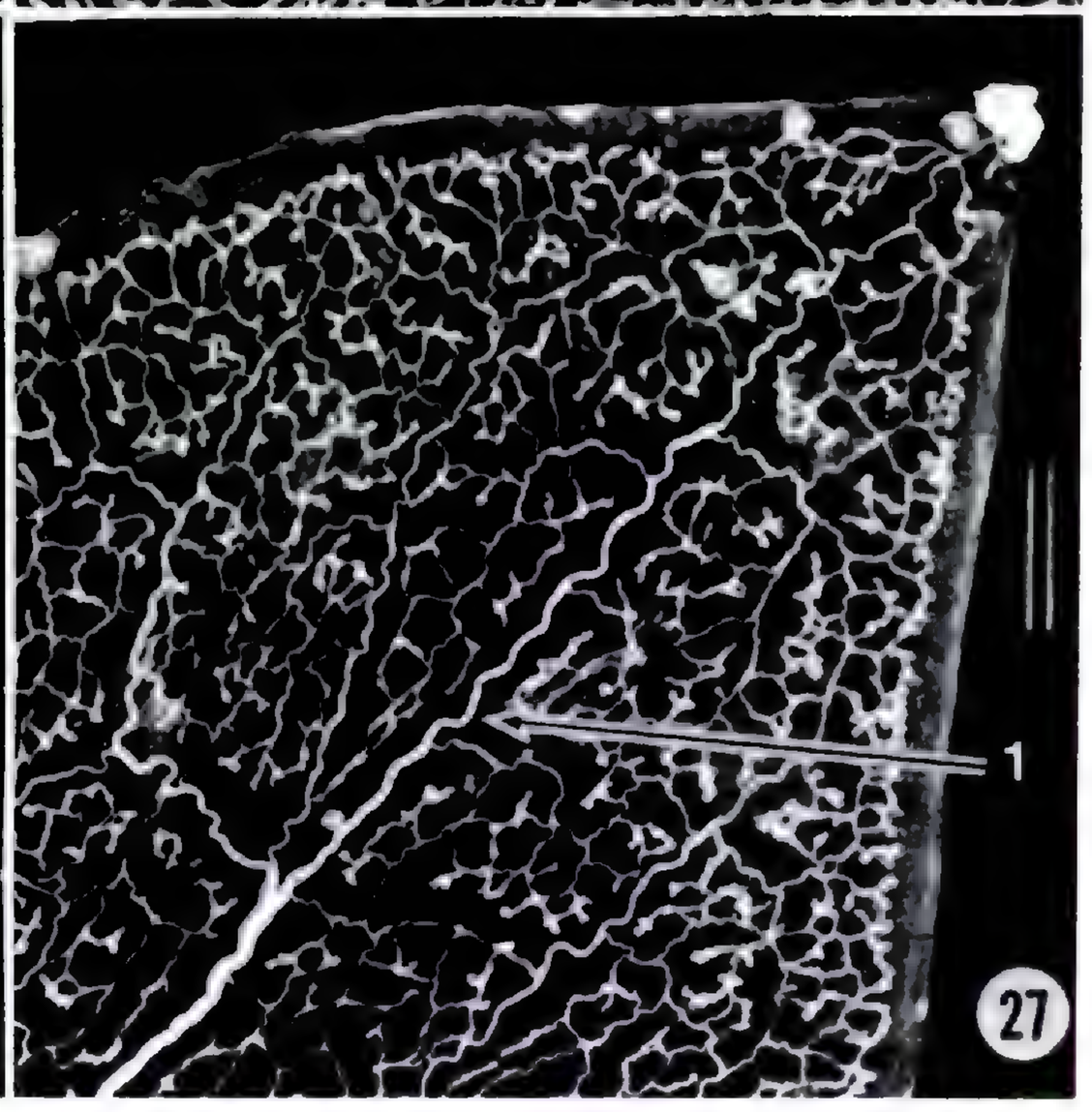




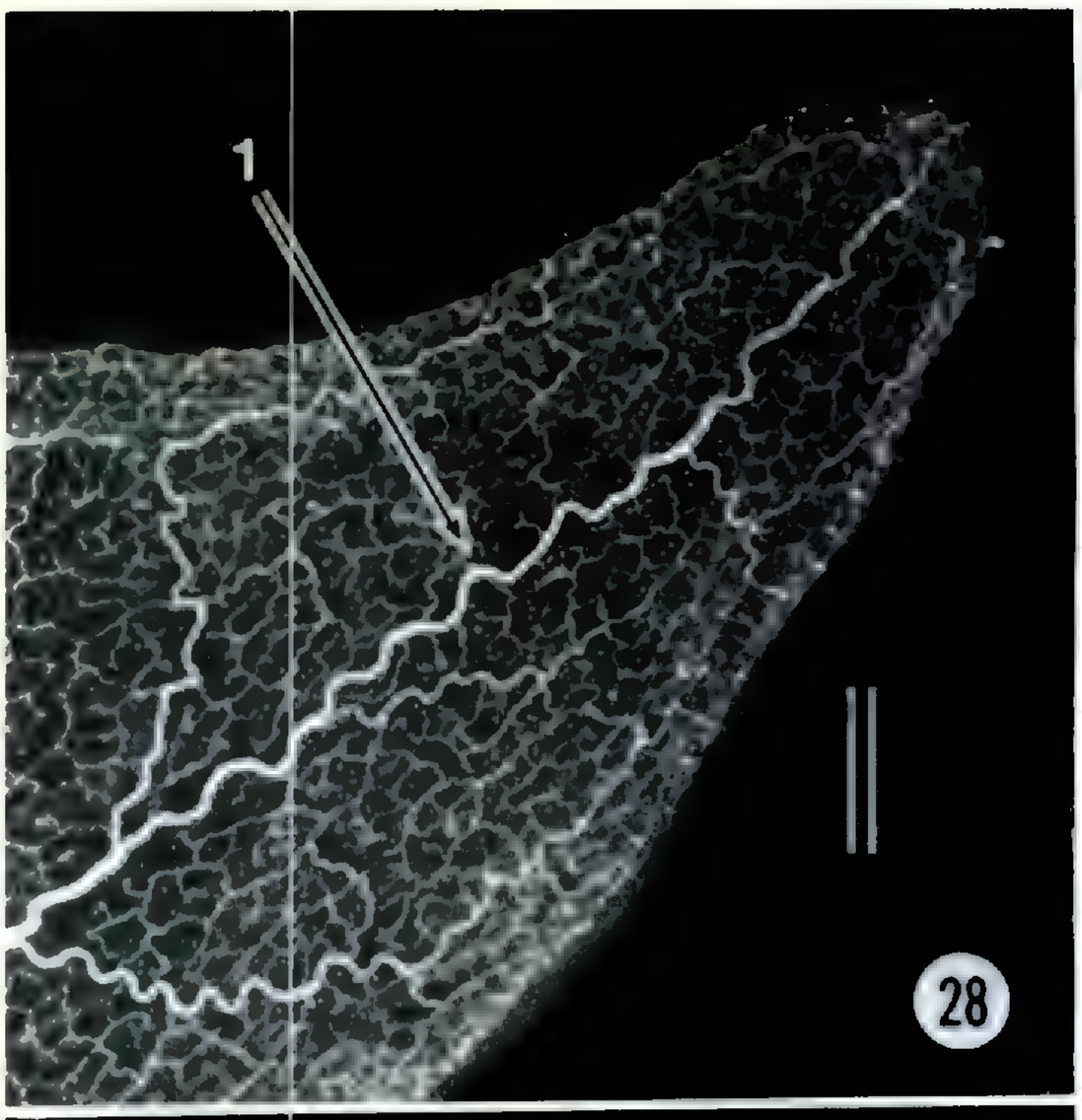


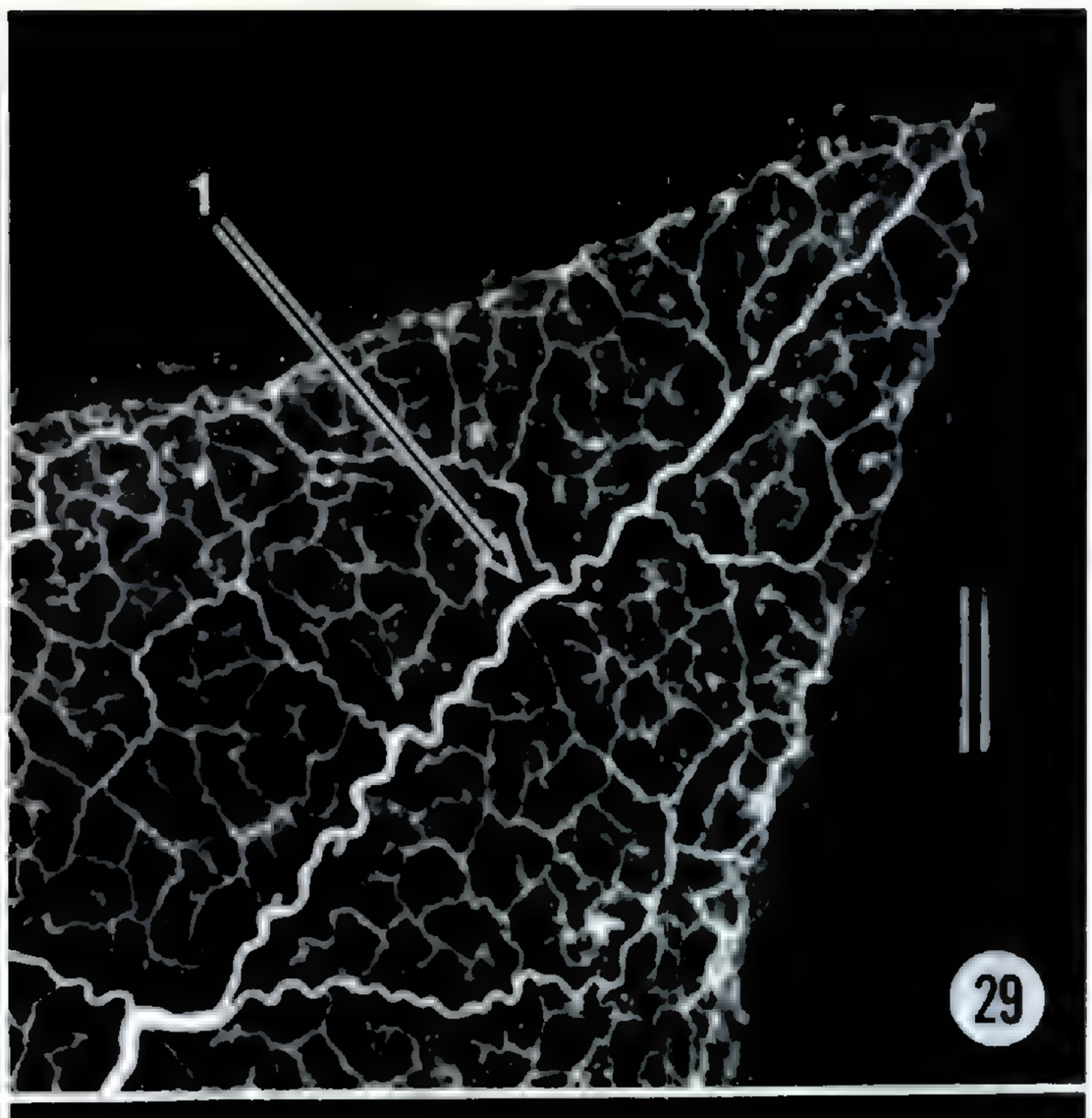


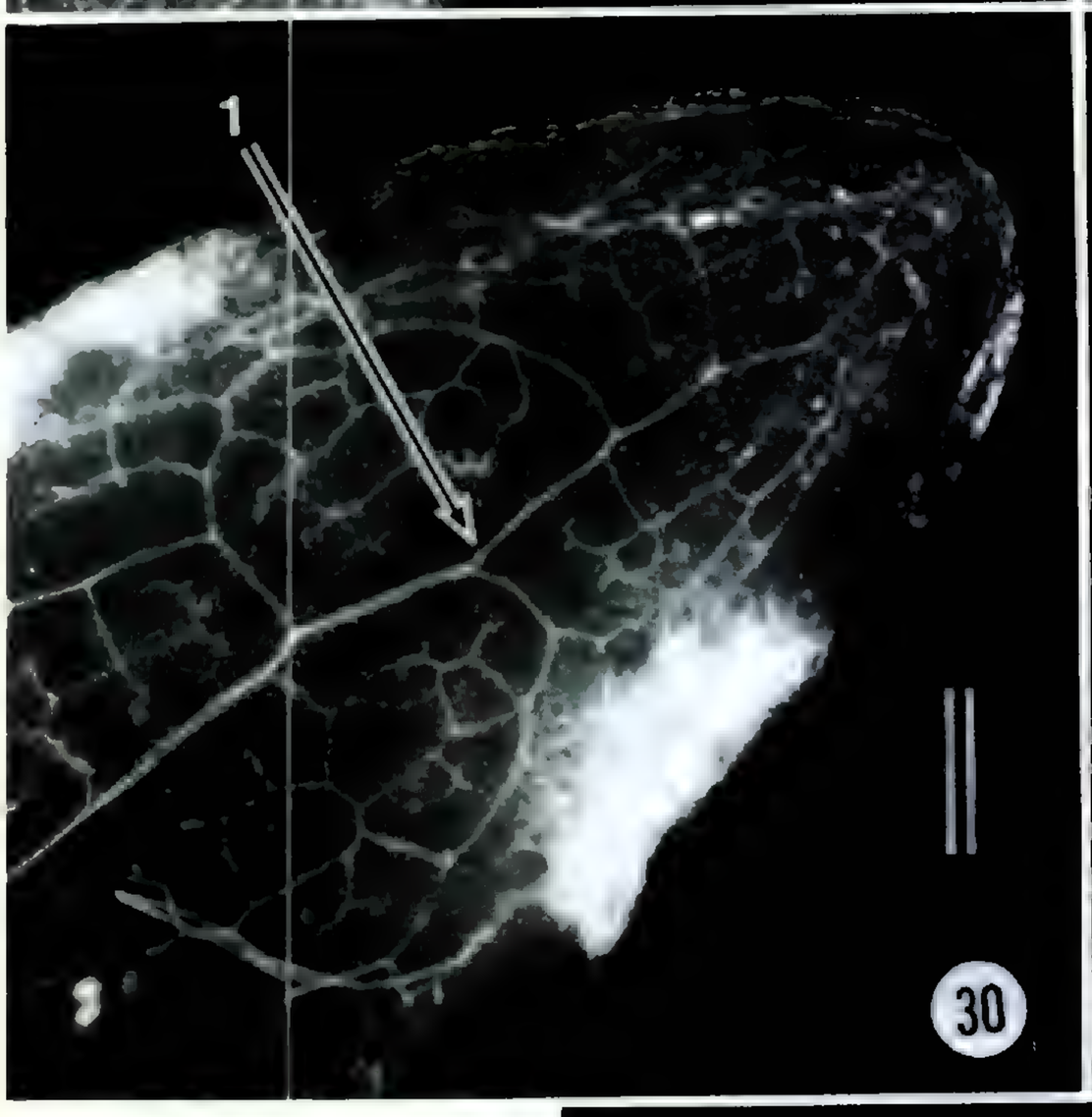


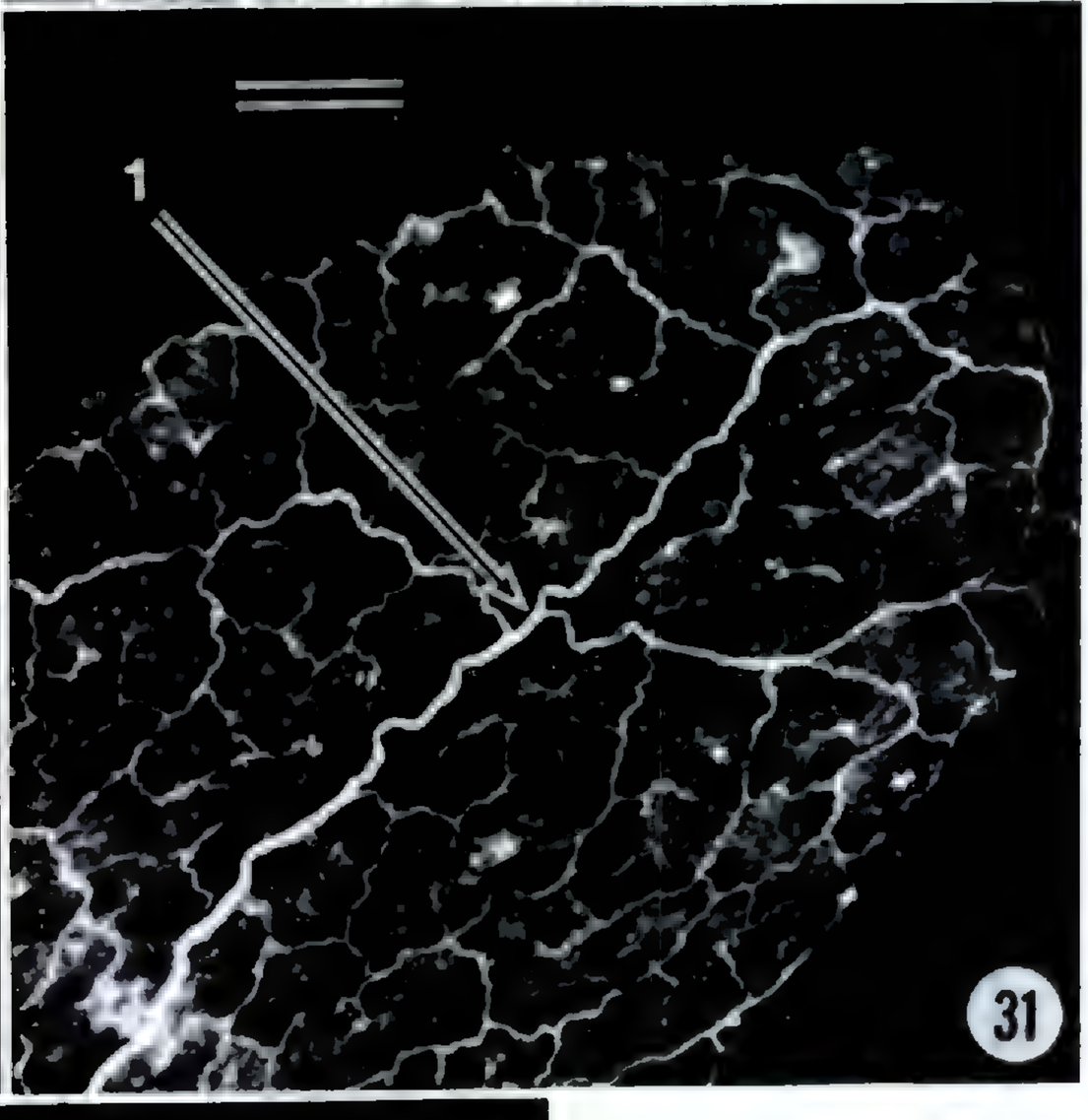


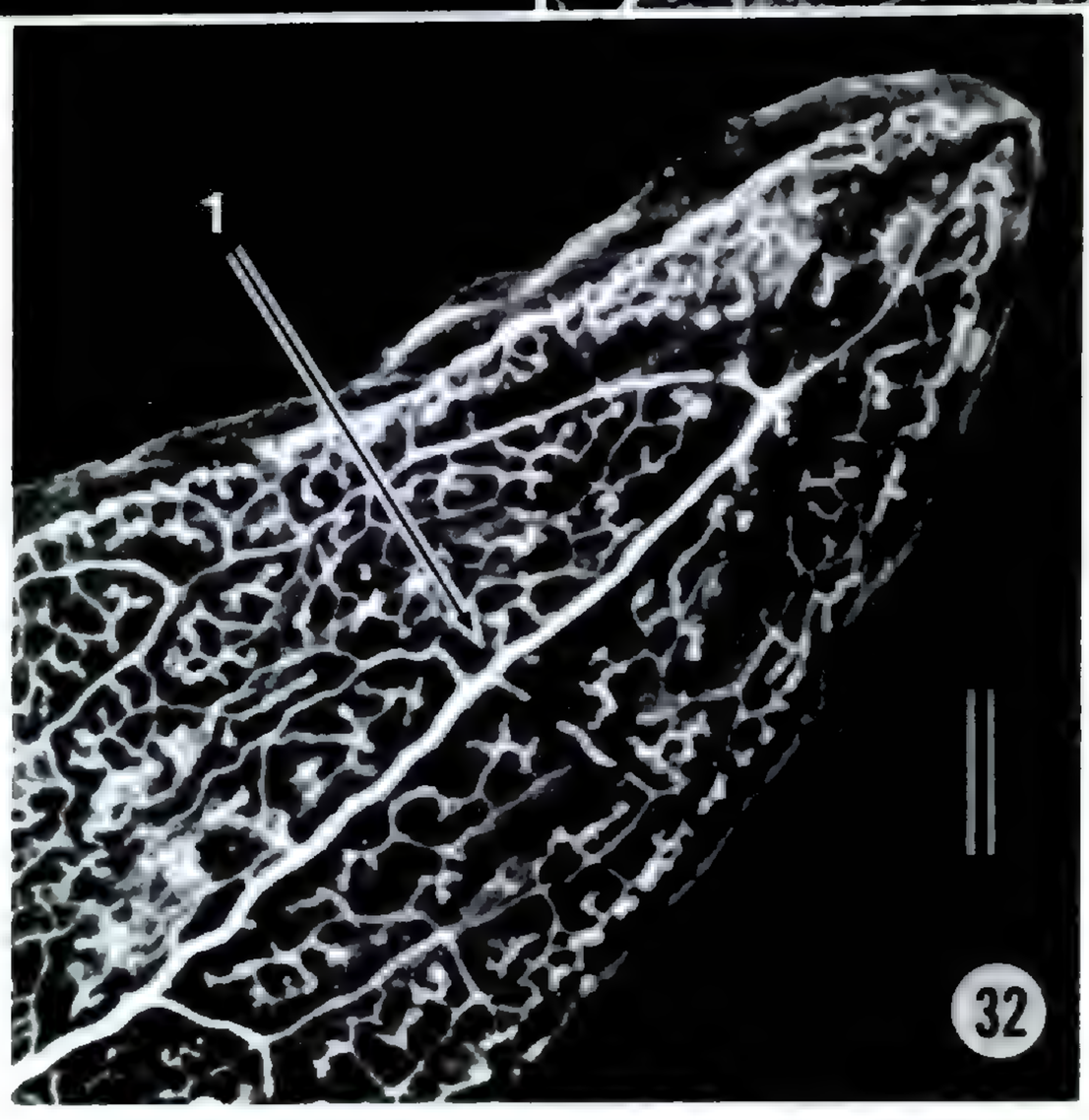
FIGURES 22–27. Cleared leaf apices of *Cistanthe* sect. *Cistanthe*. —22. *C. paniculata*. —23. *C. longiscapa*. —24. *C. guadalupensis*. —25. *C. picta* var. *picta*. —26. *C. coquimbensis*. —27. *C. grandiflora* (*Morrison et al. 16872*). Scale bars are (mm) ca. 2.7, 1.2, 1.7, 0.8, 0.8, and 0.8, respectively.



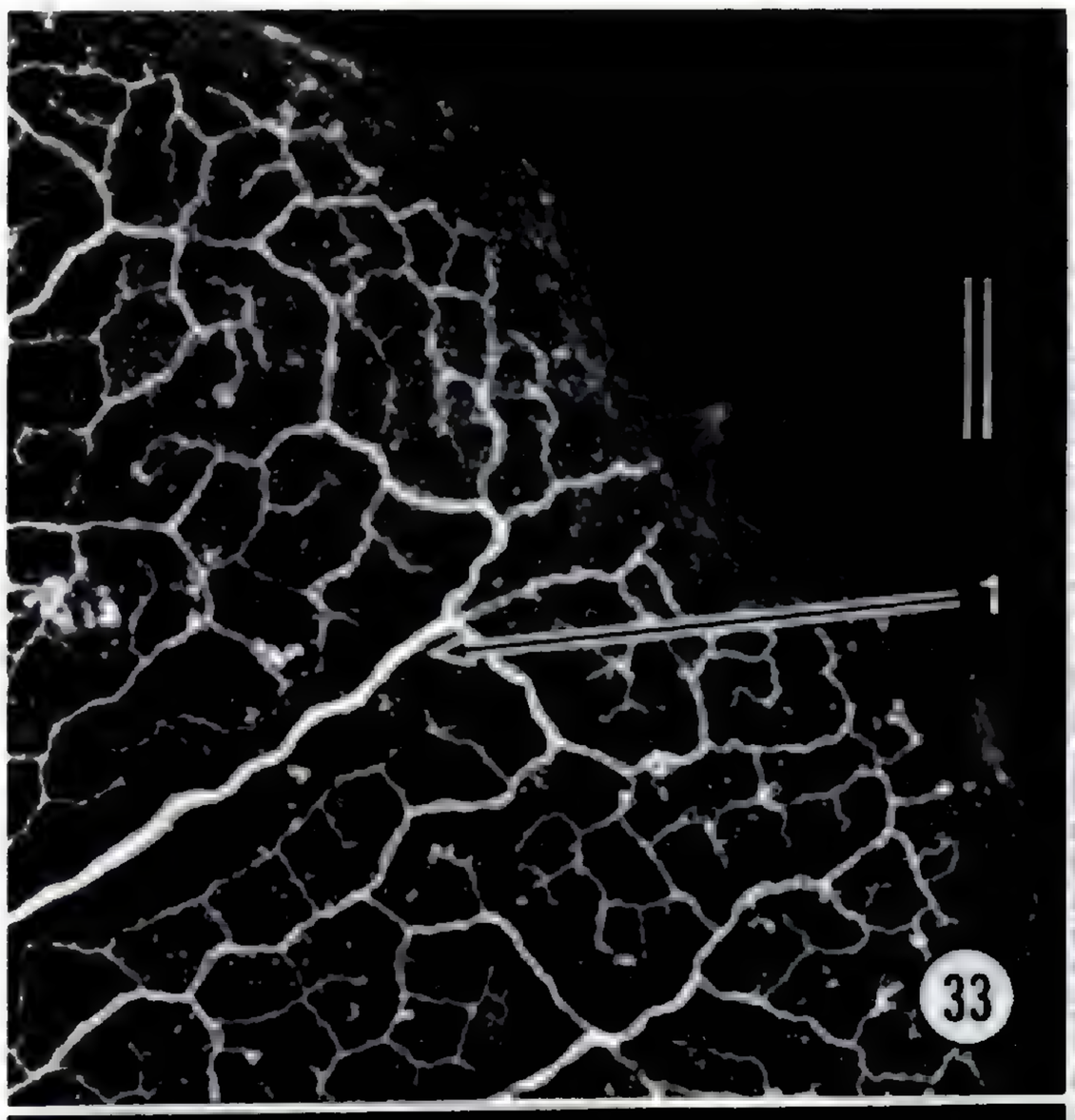


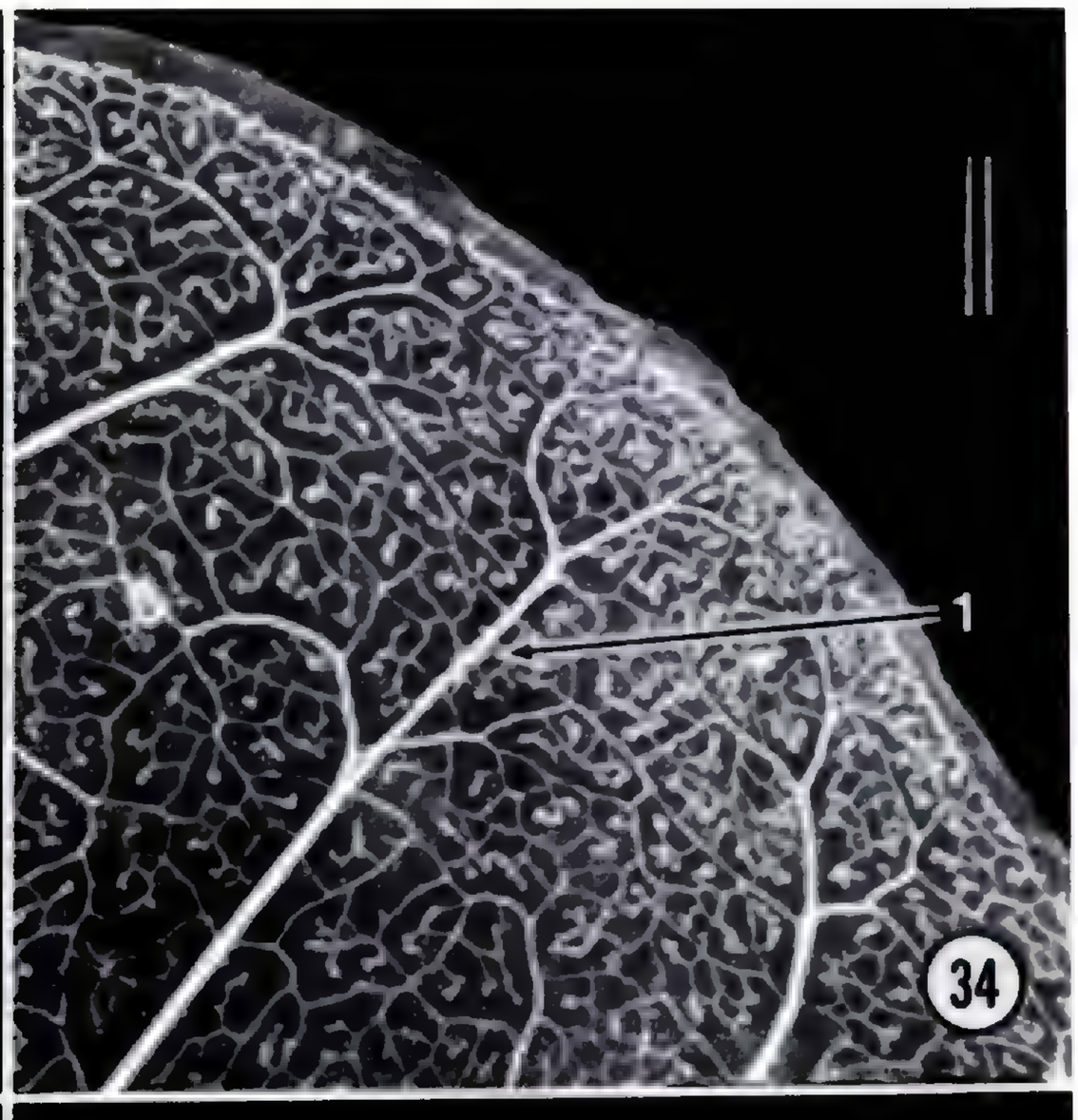


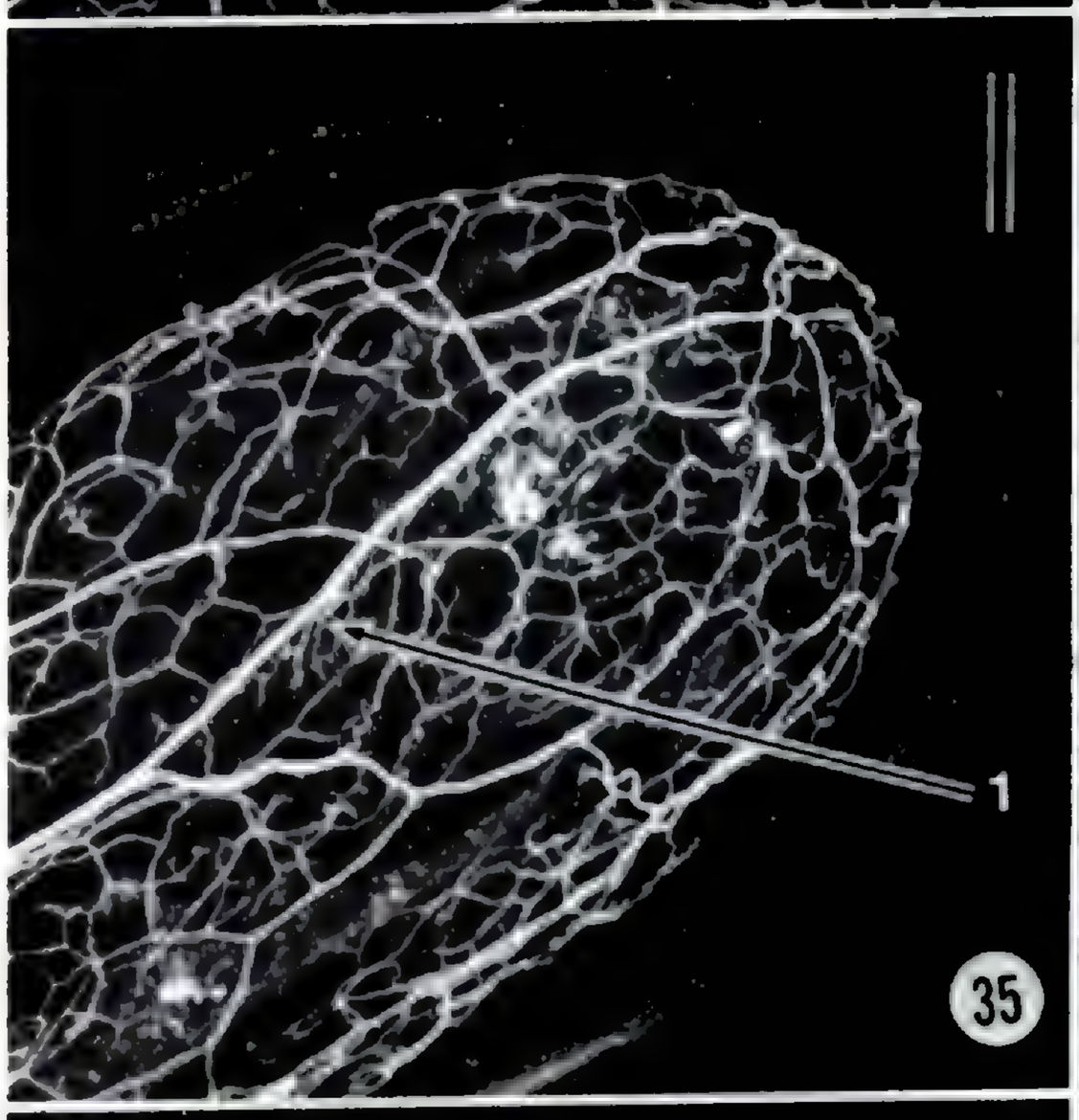


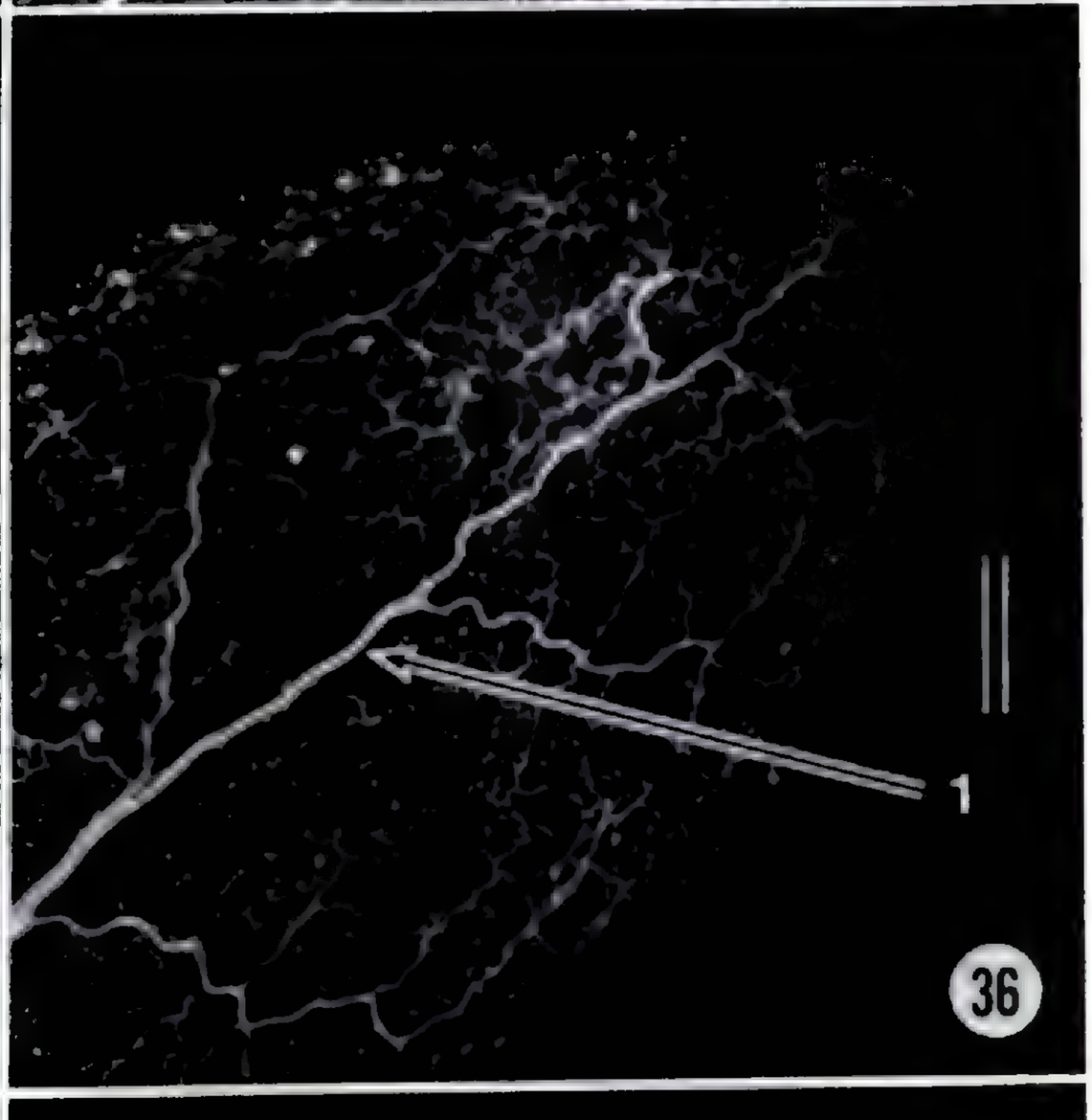


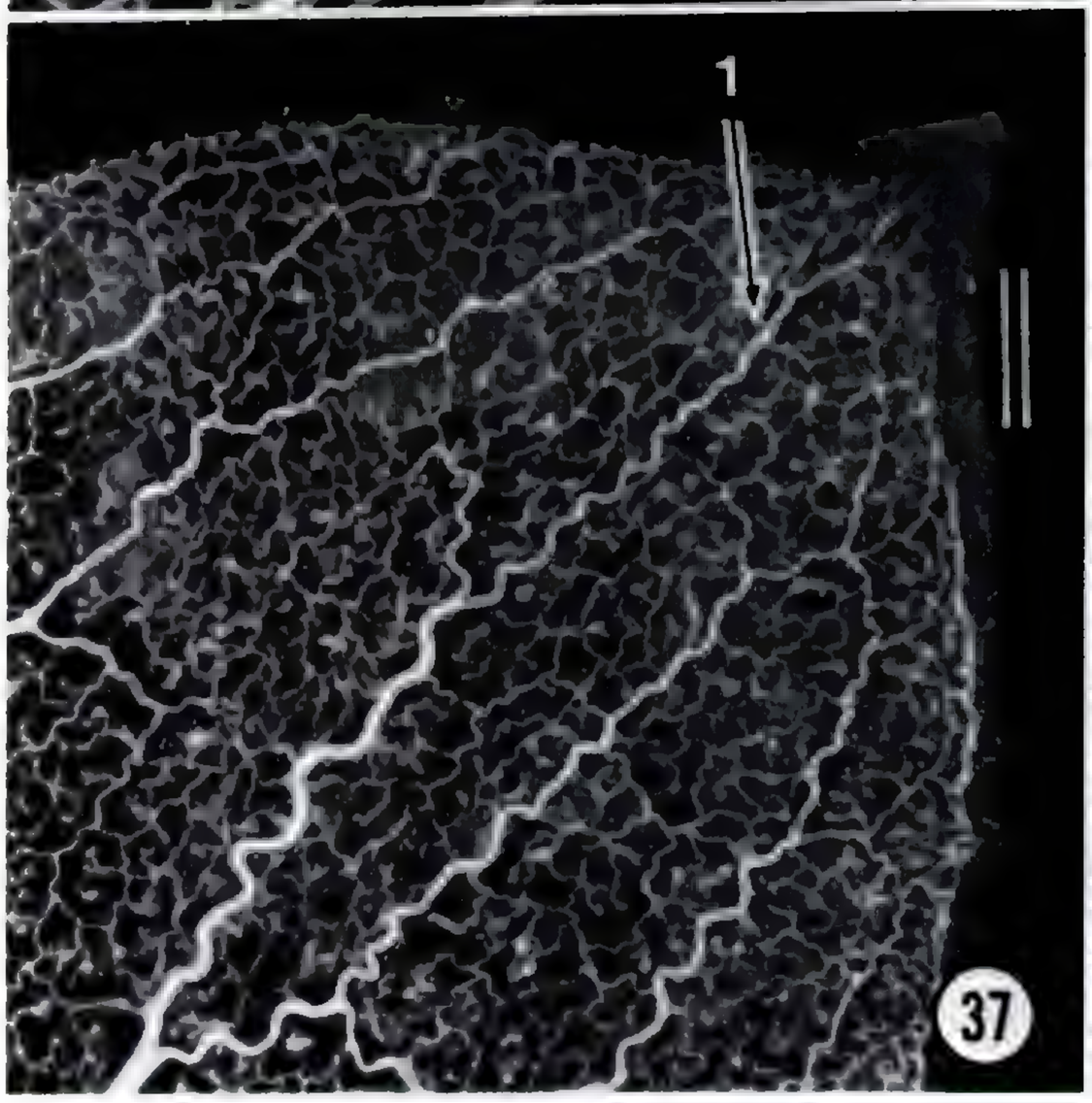
FIGURES 28–32. Cleared leaf apices of *Cistanthe* sect. *Cistanthe*.—28. *C. weberbaueri*.—29. *C.* sp. cf. *arenaria*.—30. *C. lingulata*.—31. *C.* sp. (*Zollner 9807*).—32. *C. fenzlii*. Scale bars are (mm) ca. 0.9, 0.6, 0.7, 0.8, and 0.4, respectively.

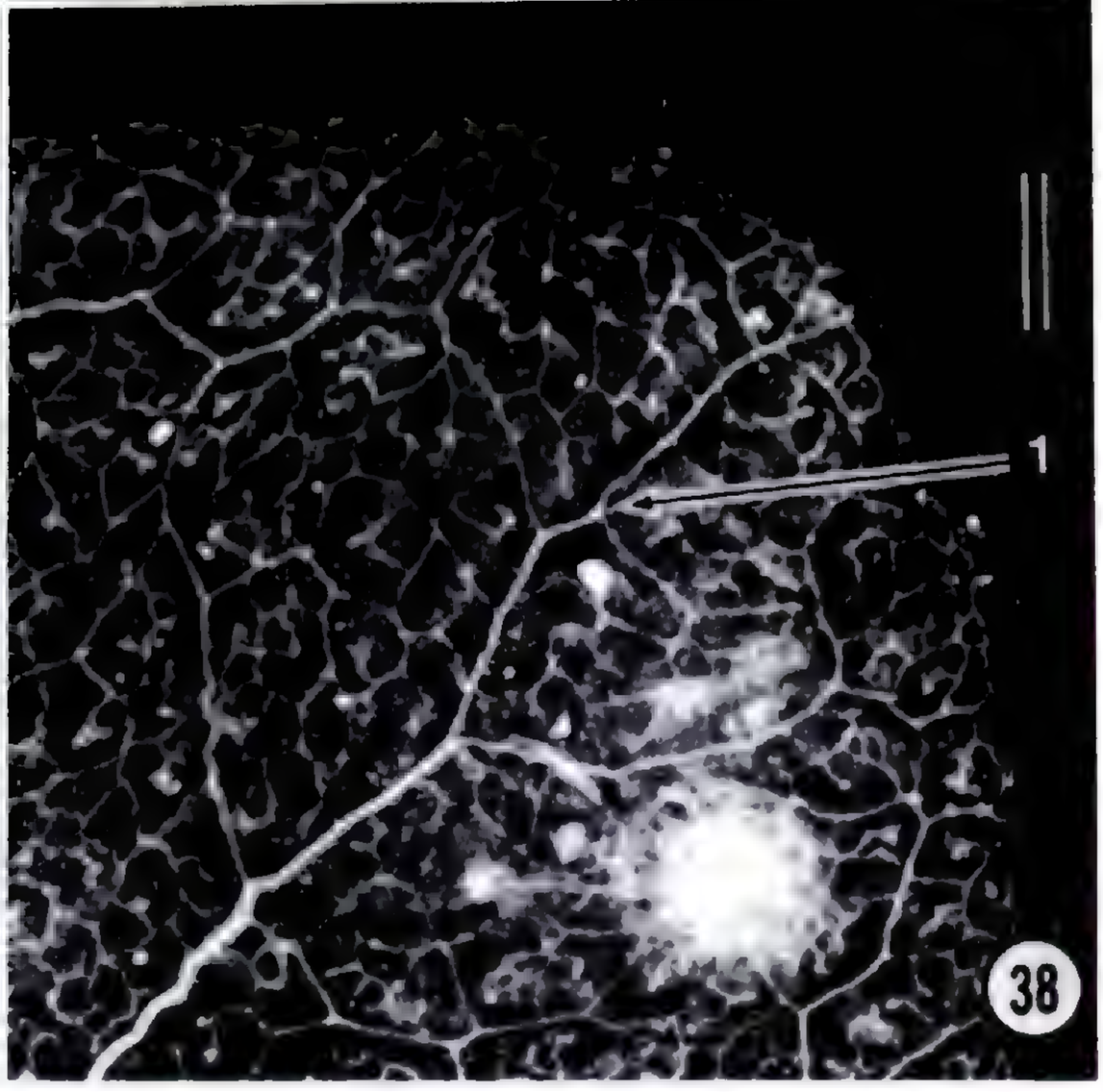




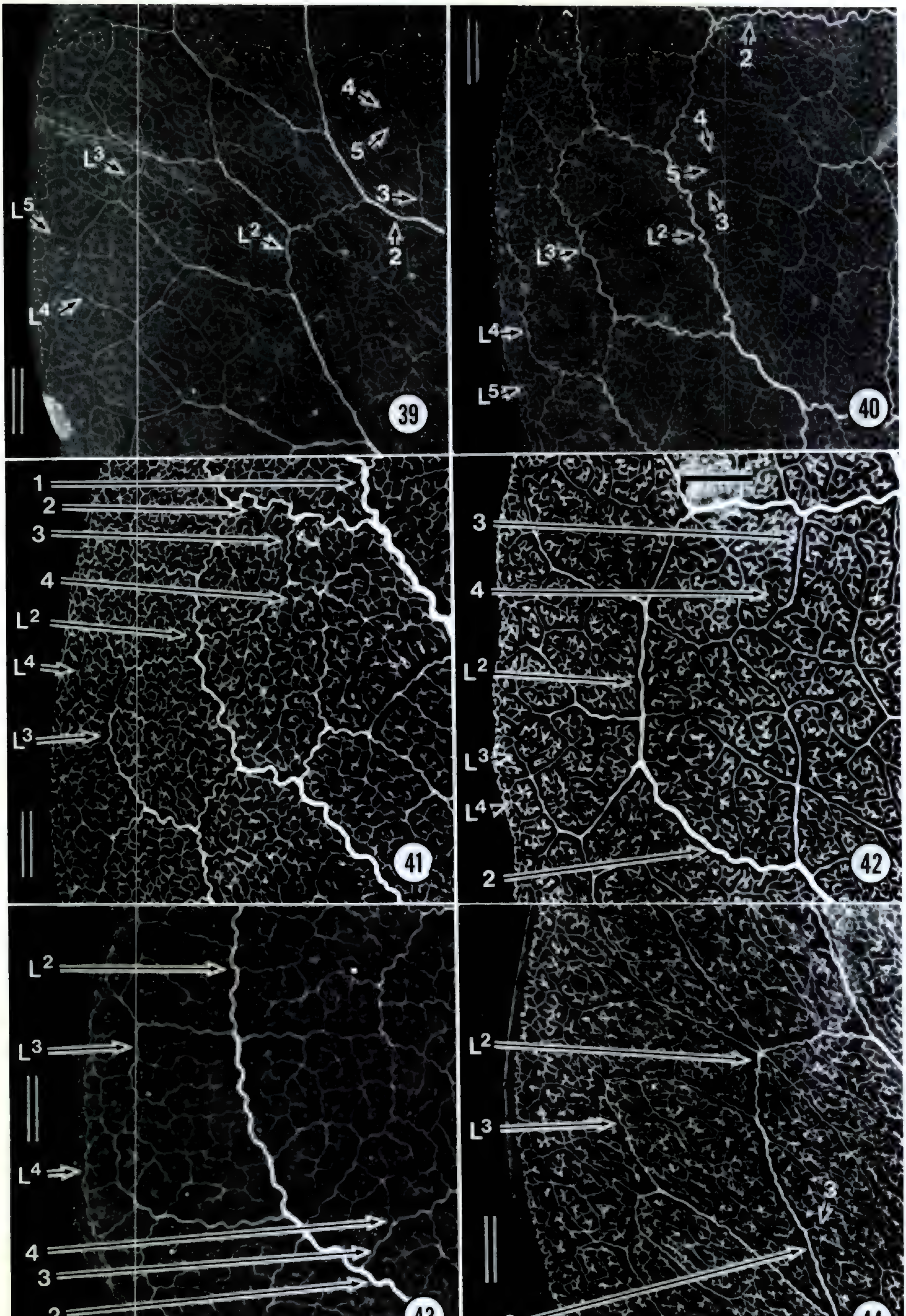




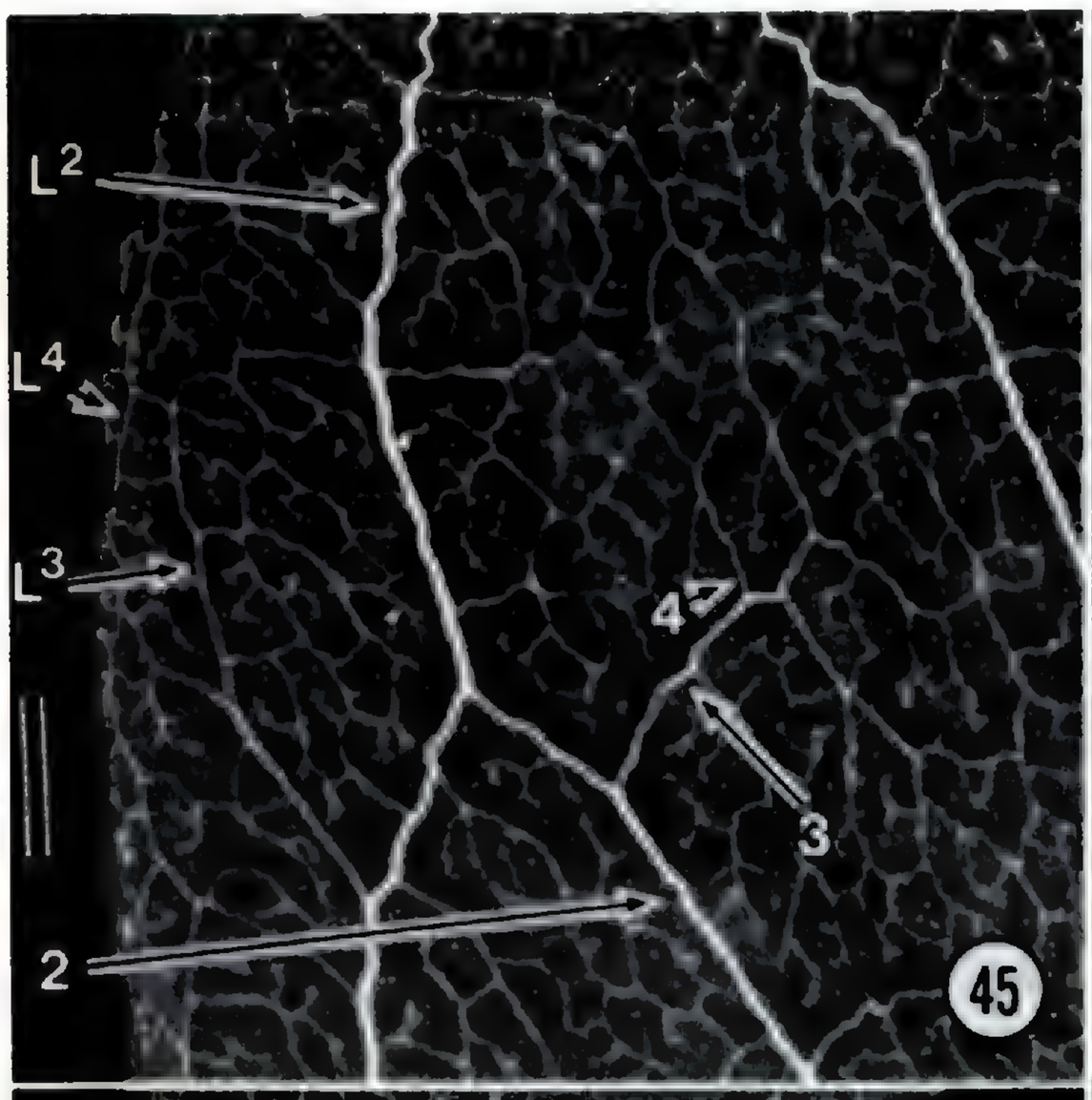


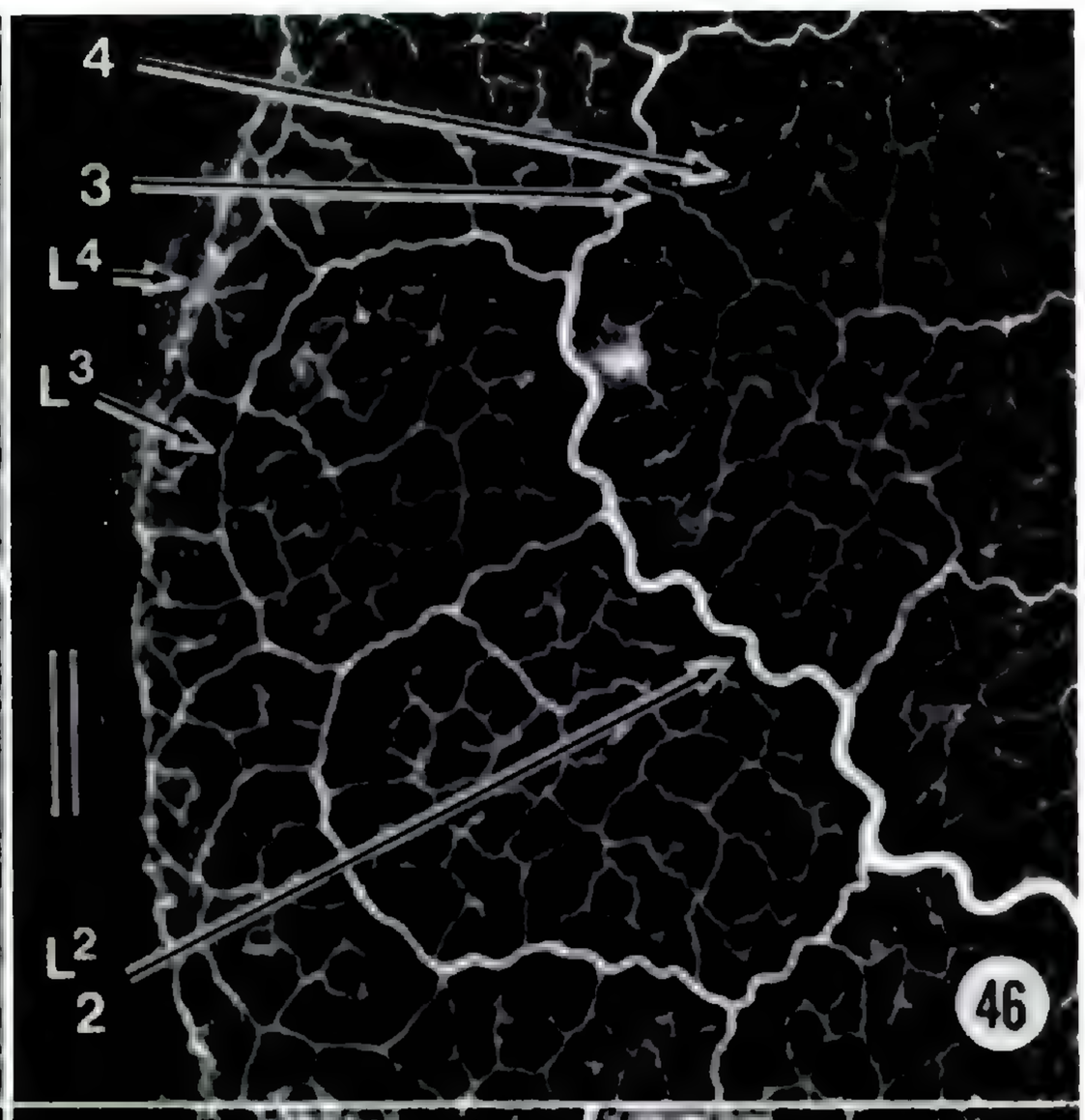


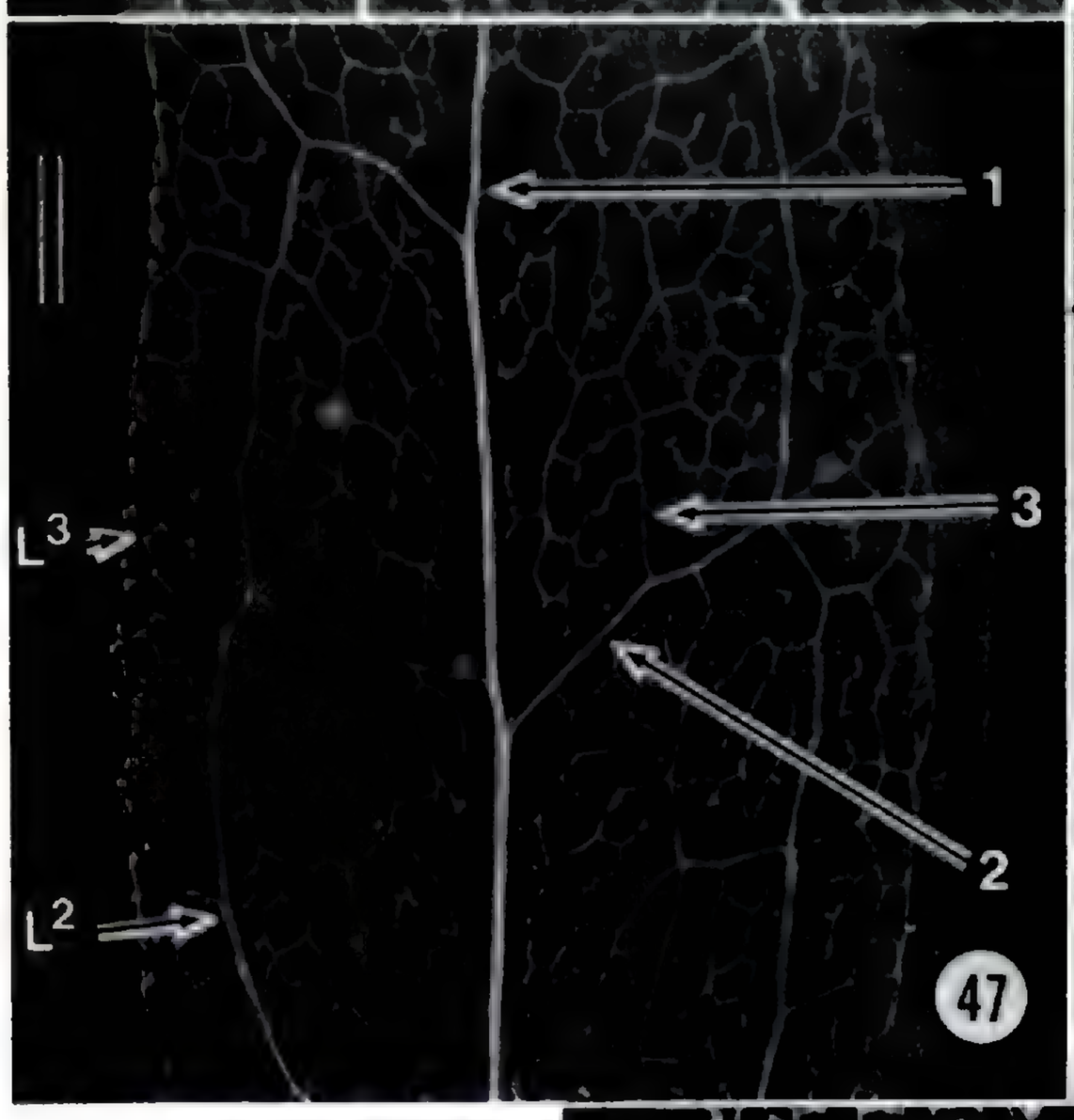
FIGURES 33–38. Cleared leaf apices of *Cistanthe* sects. *Calyptridium* (33, 34), *Amarantoideae* (35–37), and *Philippiamra* (38). —33. *C. quadripetala*. —34. *C. monosperma*. —35. *C. ambigua*. —36. *C. calycina*. —37. *C. salsoloides*. —38. *C. celosioides*. Scale bars are (mm) ca. 0.9, 1.0, 1.0, 0.7, 0.8, and 0.6, respectively.

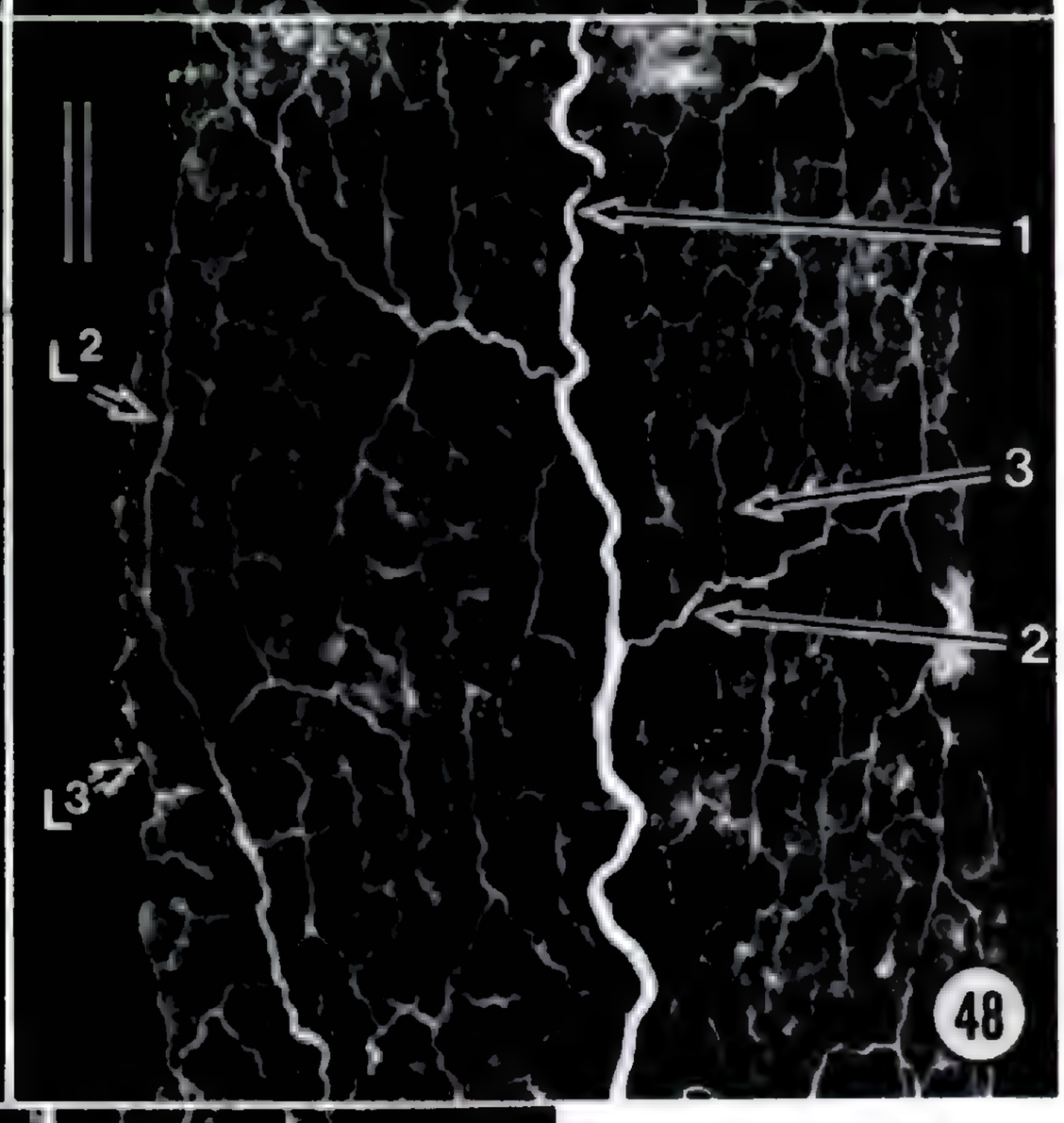


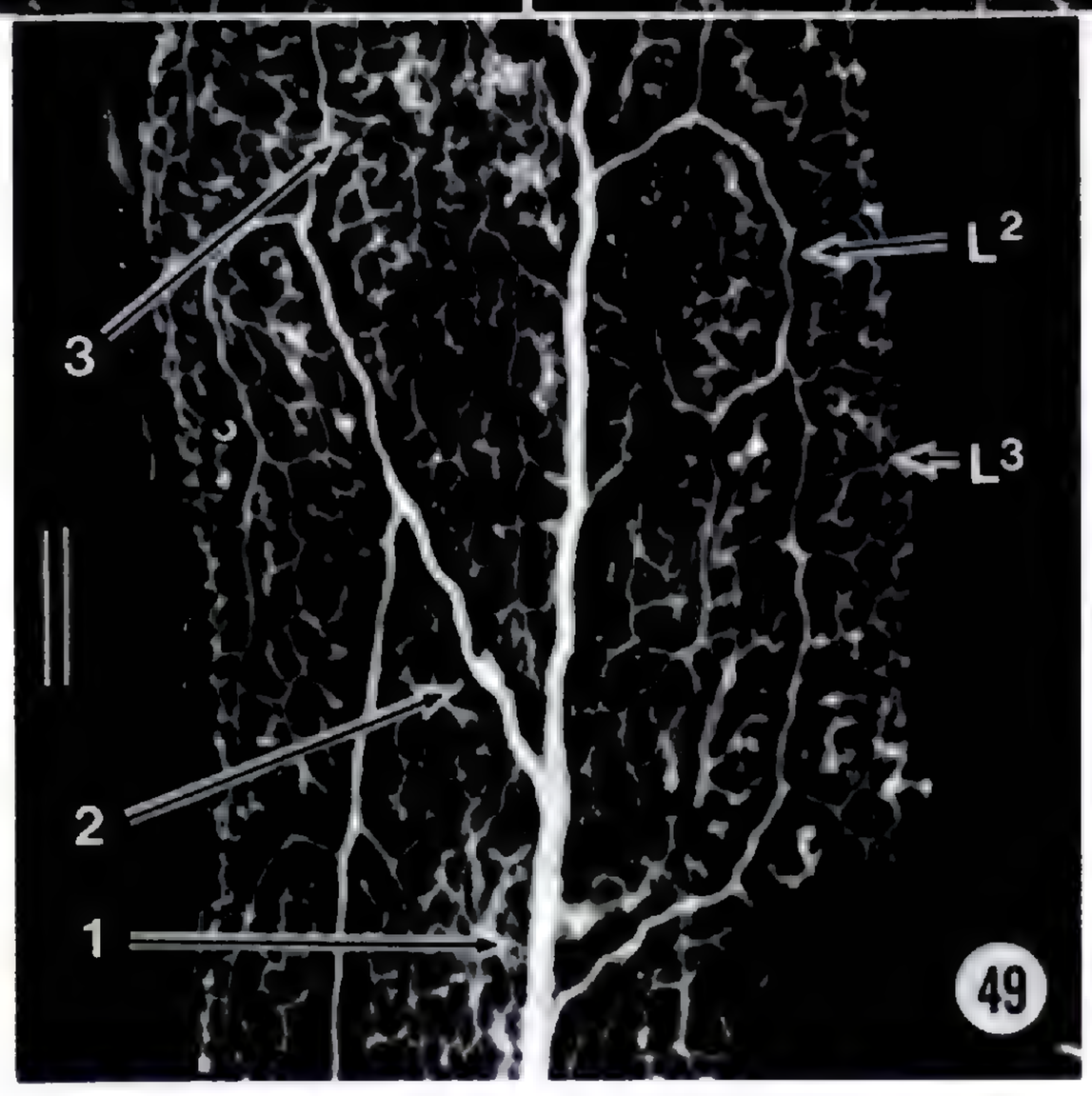
FIGURES 39–44. Cleared leaf central-marginal portions of *Cistanthe* sect. *Cistanthe*.—39. *C. paniculata*. In Figures 39 and 40, the fourth- and fifth-order veins are difficult to discern, but their existence can be inferred by extrapolation from the tertiary veins. The fourth-order veins form the reticulum adjacent to the tertiary veins, and the fifth-order veins traverse the areoles formed by the fourth-order veins and give rise to the free-ending veinlets.—40. *C. longiscapa*.—41. *C. guadalupensis*.—42. *C. picta* var. *picta*.—43. *C. coquimbensis*.—44. *C. grandiflora* (*Werdermann 495*). Scale bars are (mm) ca. 2.2, 1.4, 1.7, 0.9, 0.8, and 1.6, respectively.



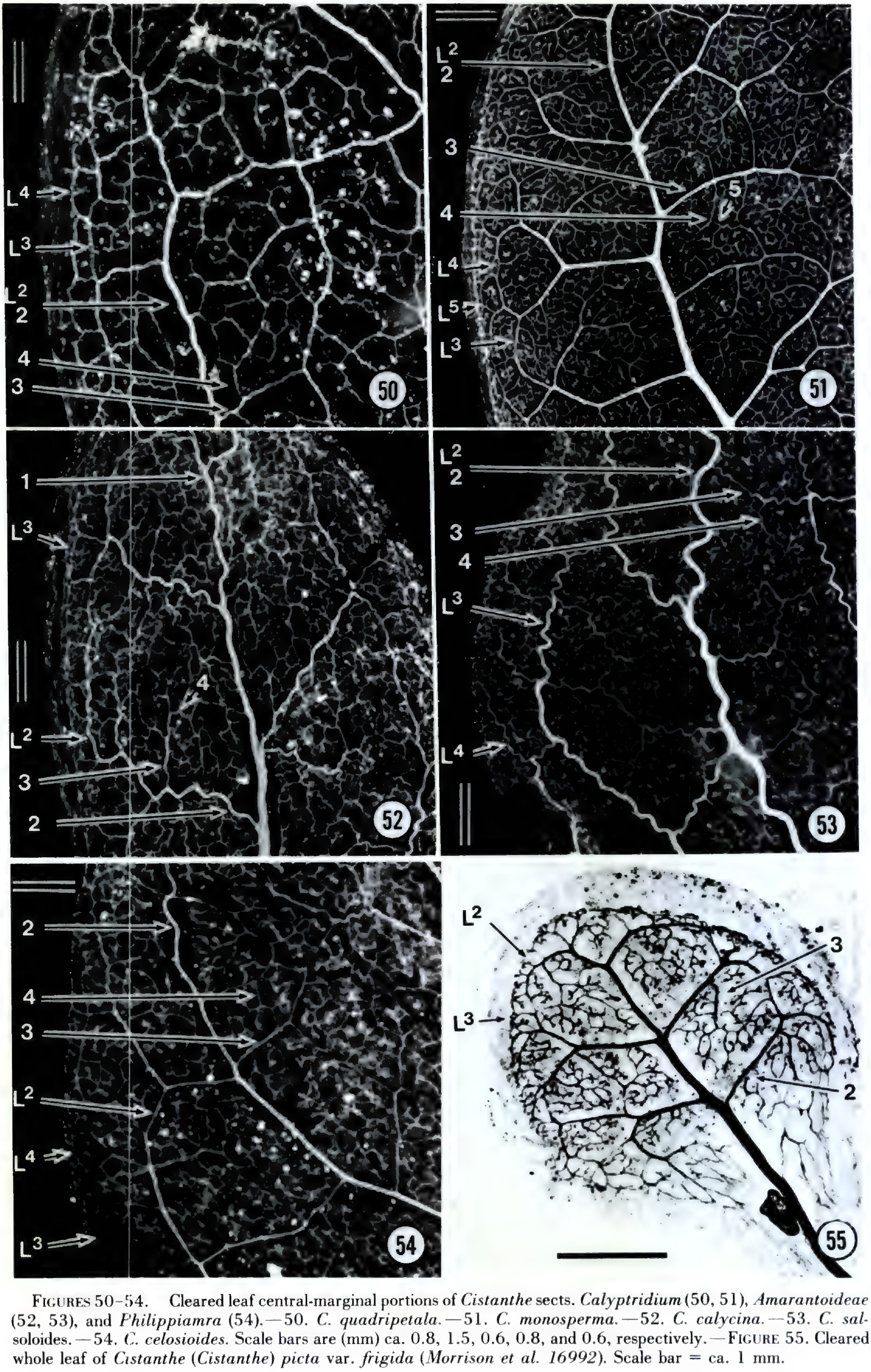




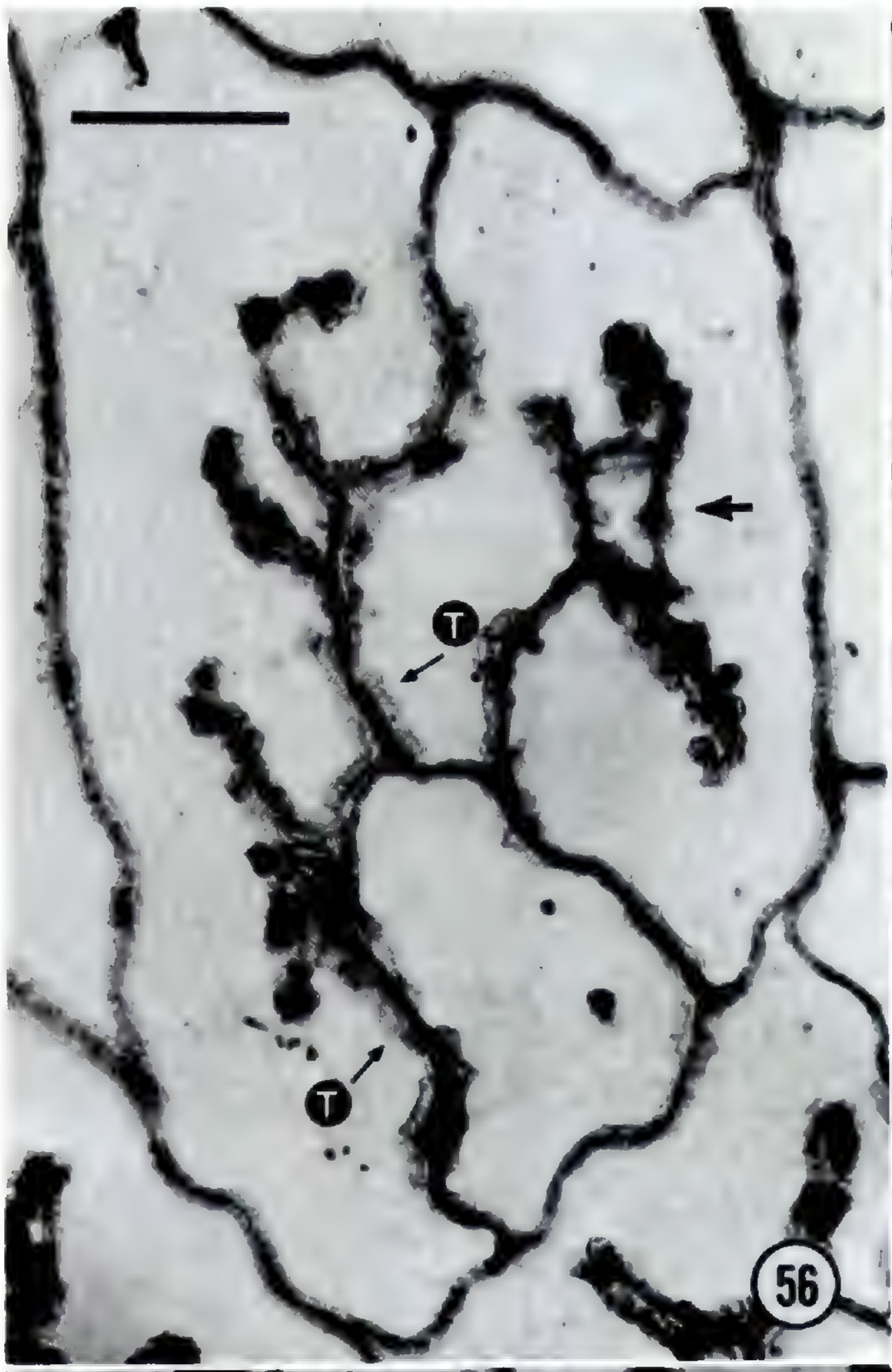


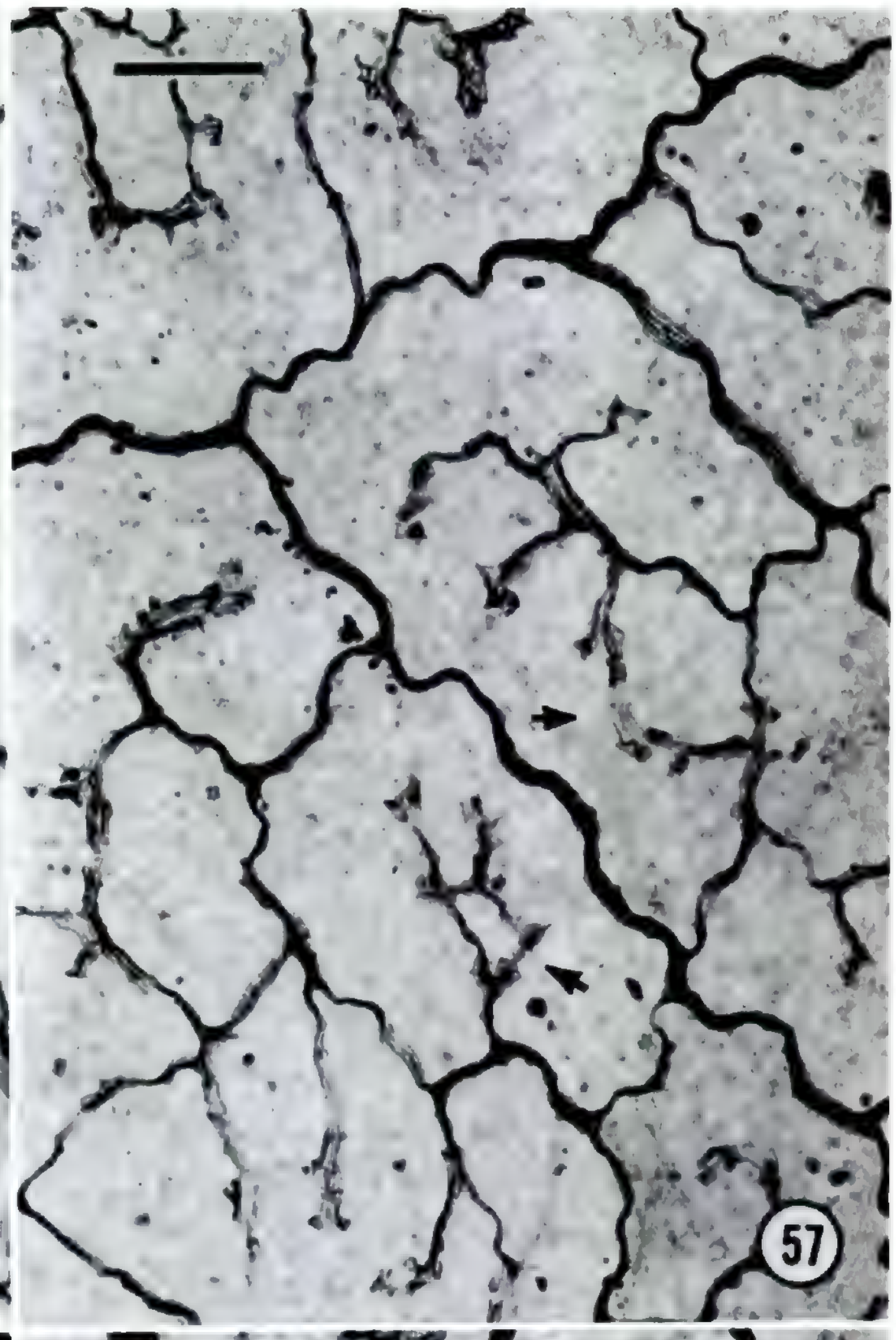


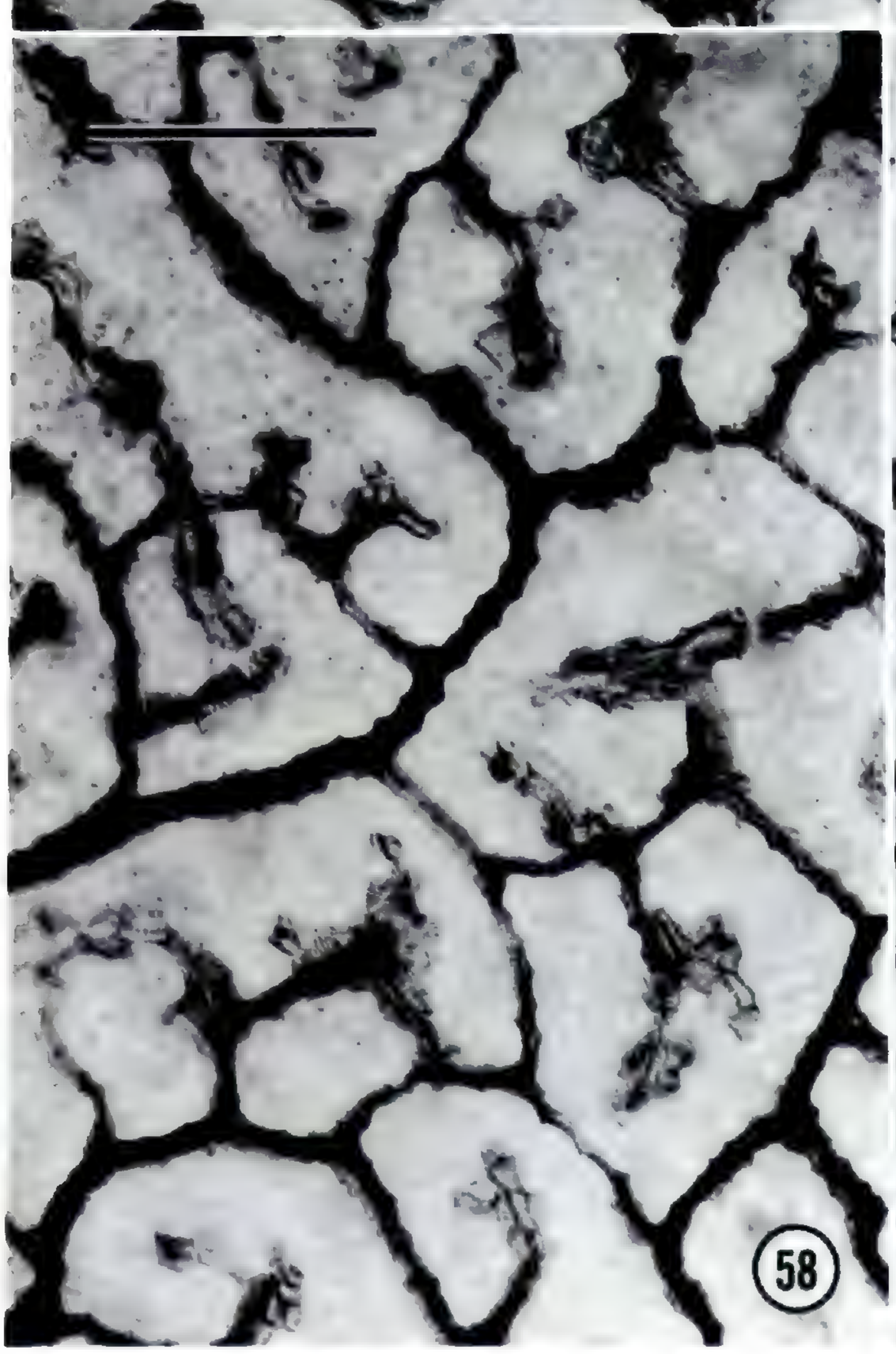
FIGURES 45–49. Cleared leaf central-marginal portions of *Cistanthe* sect. *Cistanthe*.—45. *C. weberbaueri*.—46. *C.* sp. cf. *arenaria*.—47. *C. lingulata*.—48. *C.* sp. (*Zollner 9807*).—49. *C. fenzlii*. Scale bars are (mm) ca. 0.7, 0.5, 1.1, 0.8, and 1.6, respectively.

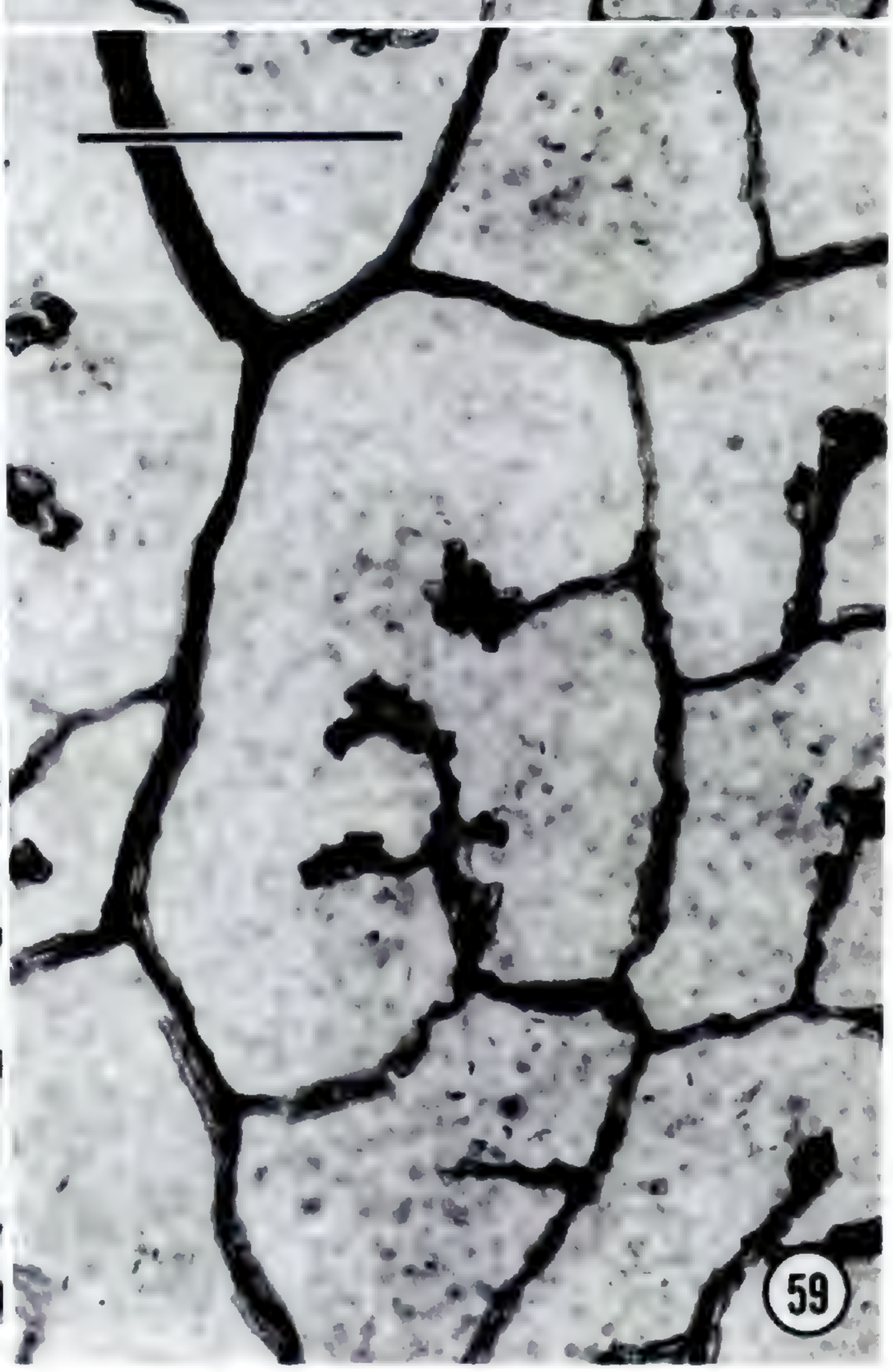


FIGURES 50–54. Cleared leaf central-marginal portions of *Cistanthe* sects. *Calyptridium* (50, 51), *Amarantoideae* (52, 53), and *Philippiamra* (54).—50. *C. quadripetala.*—51. *C. monosperma.*—52. *C. calycina.*—53. *C. salsoloides.*—54. *C. celosioides.* Scale bars are (mm) ca. 0.8, 1.5, 0.6, 0.8, and 0.6, respectively.—FIGURE 55. Cleared whole leaf of *Cistanthe* (*Cistanthe*) *picta* var. *frigida* (*Morrison et al. 16992*). Scale bar = ca. 1 mm.

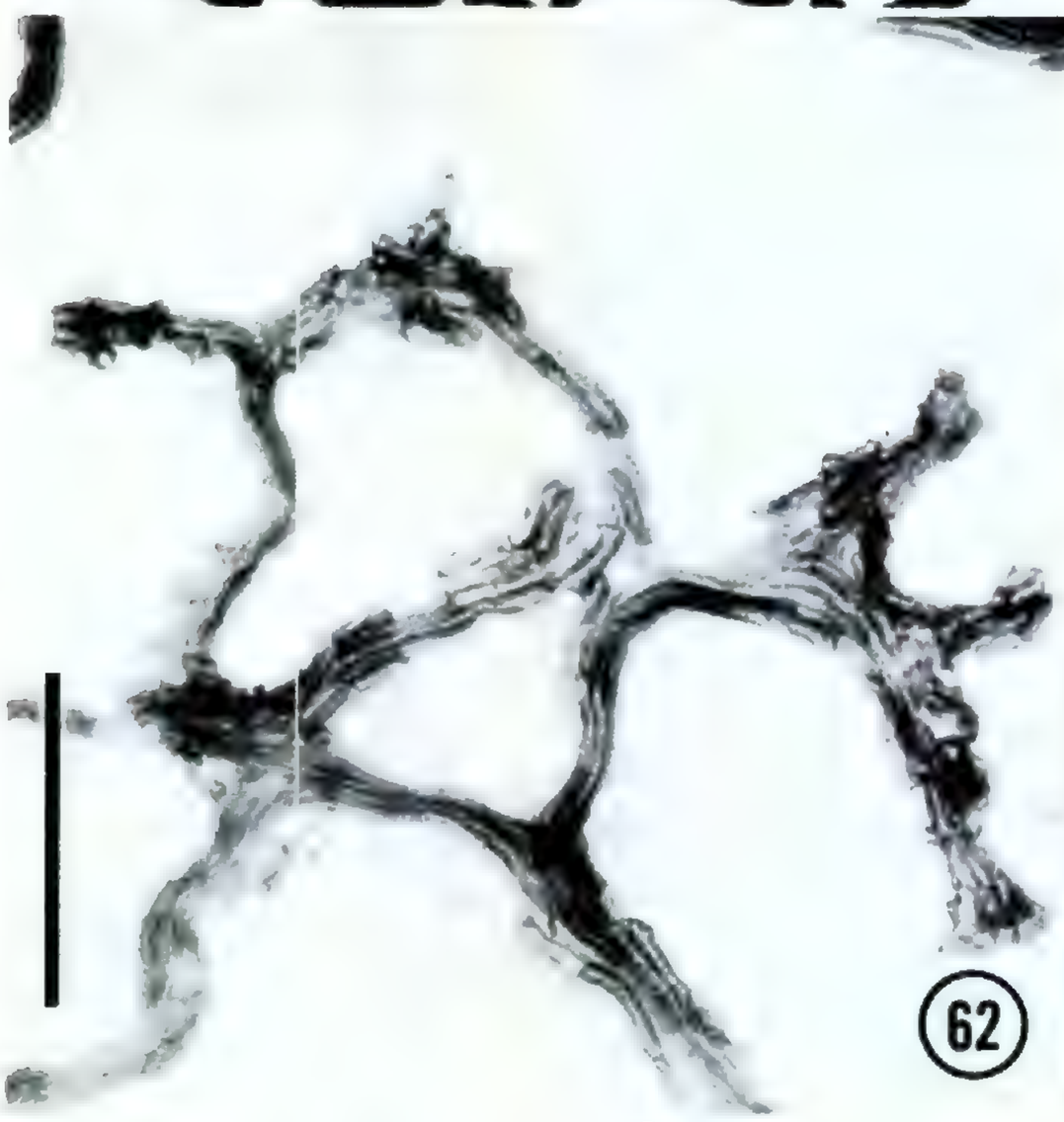


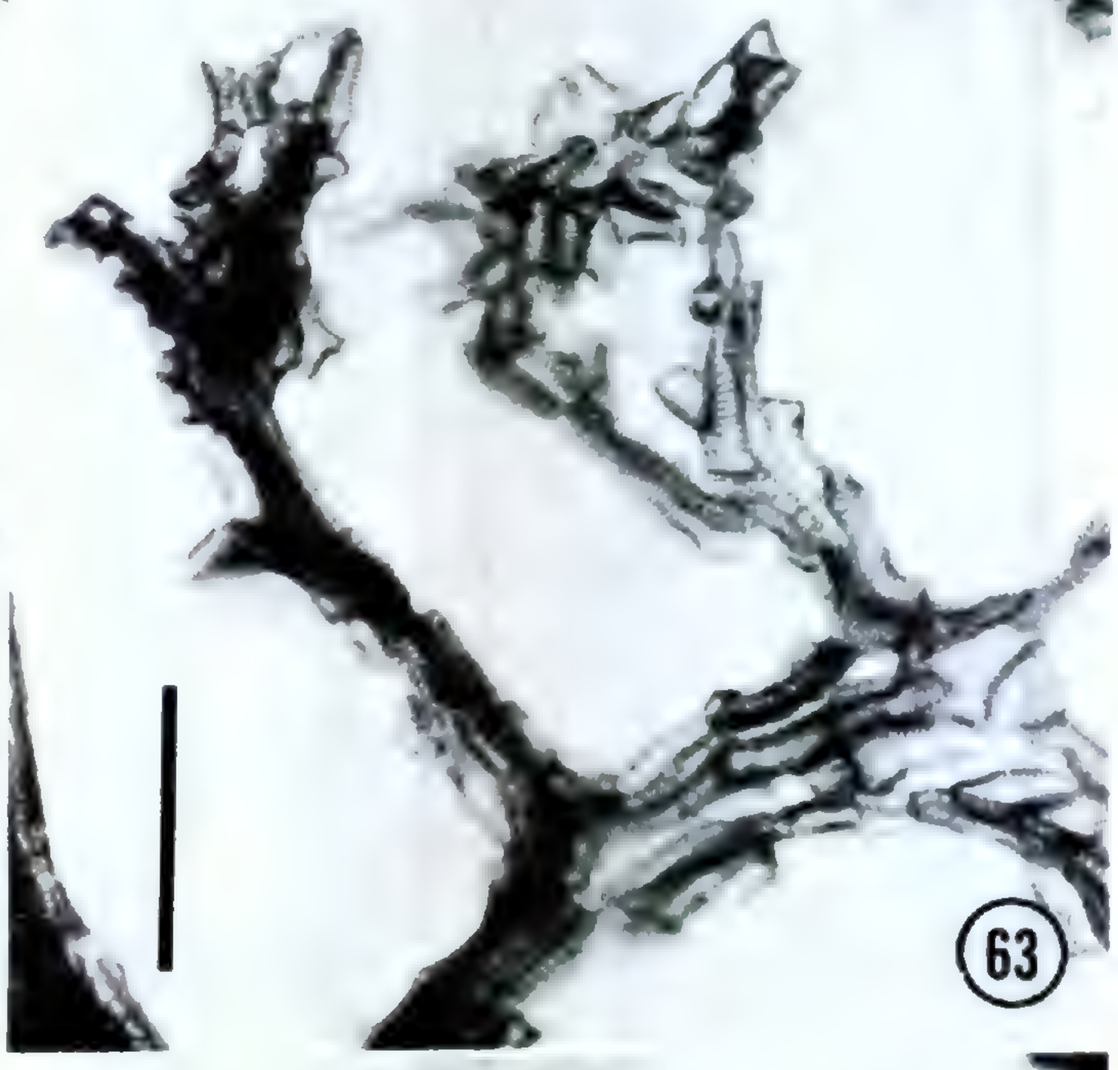


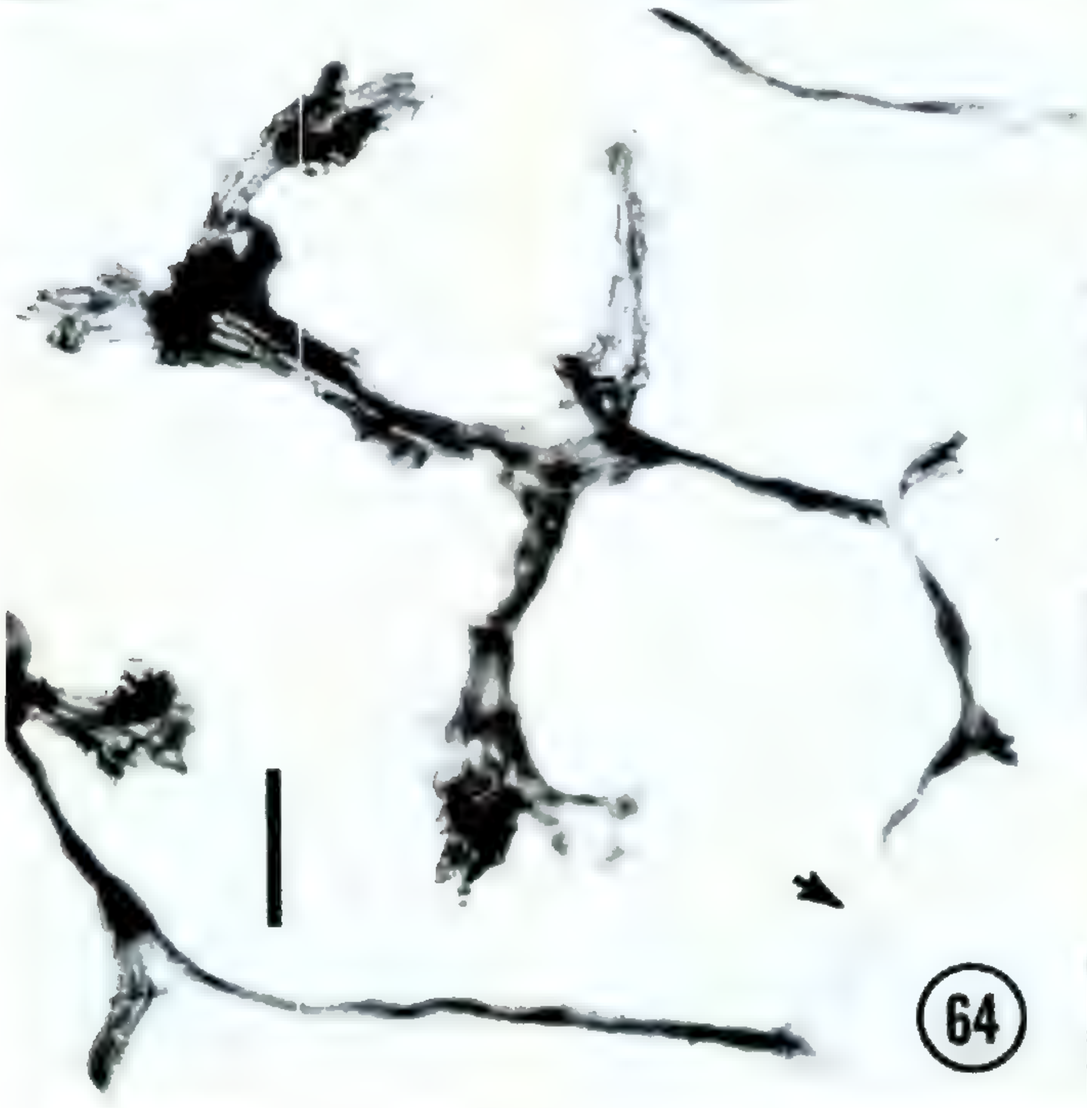


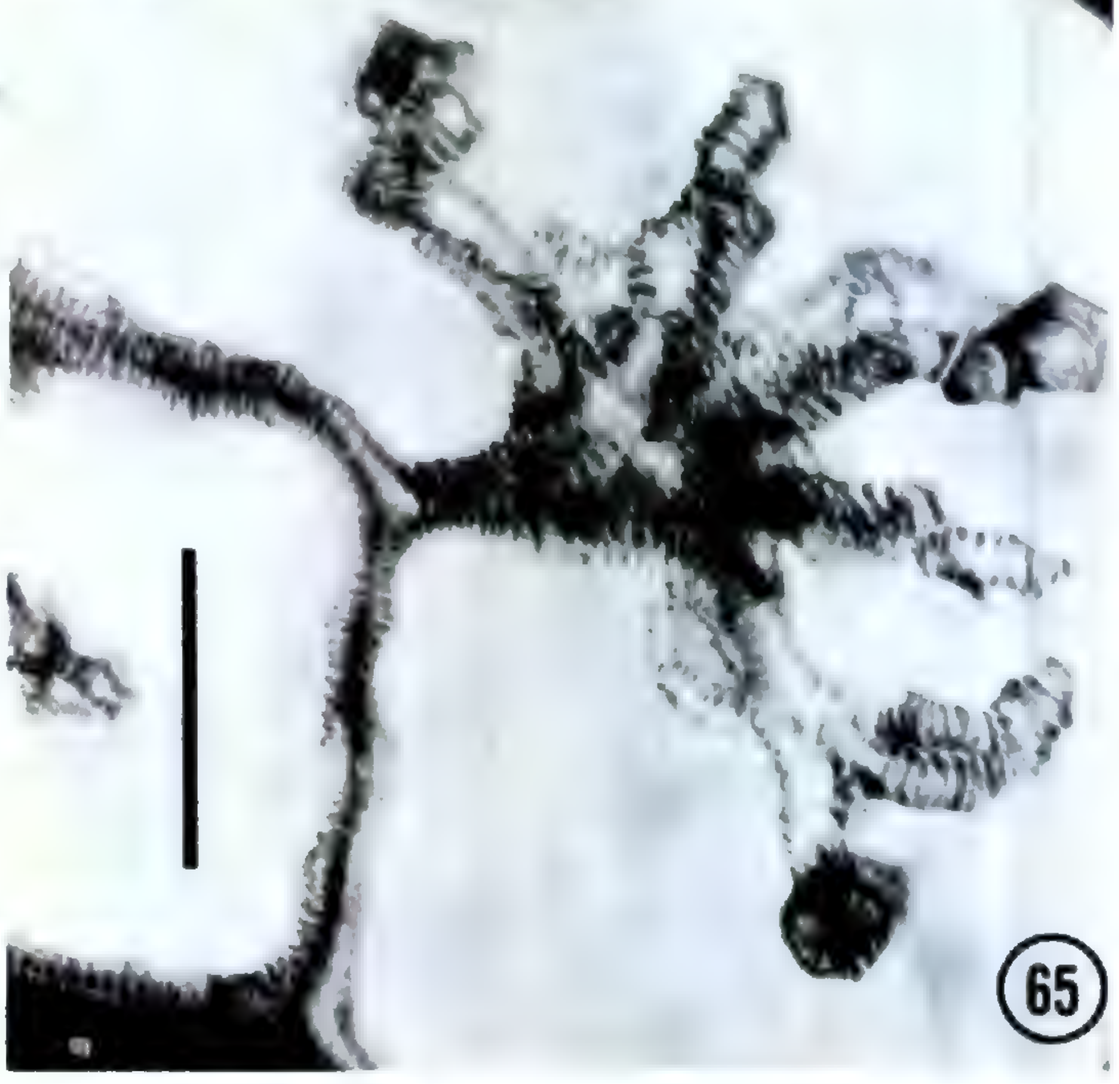


FIGURES 56–59. Fine venation features in *Cistanthe*. 56. Ultimate venation in *C.* (*Cistanthe*) *grandiflora* (*West 3959*). Note the "tracheoids" (T) along the fine veins and the coalescence of veinlet branches (large arrowhead).—57. Ultimate venation and coalesced veinlets (arrows) in *C.* (*Cistanthe*) *coquimbensis* (*Werdermann 881*).—58. Ultimate venation in *C.* (*Cistanthe*) *picta* var. *picta* (*Hutchinson 98*). Note the lack of sinuous veins.—59. Ultimate venation in *C.* (*Philippiamra*) *celosioides* (*Worth & Morrison 15820*). Scale bars = ca. 200 μm.

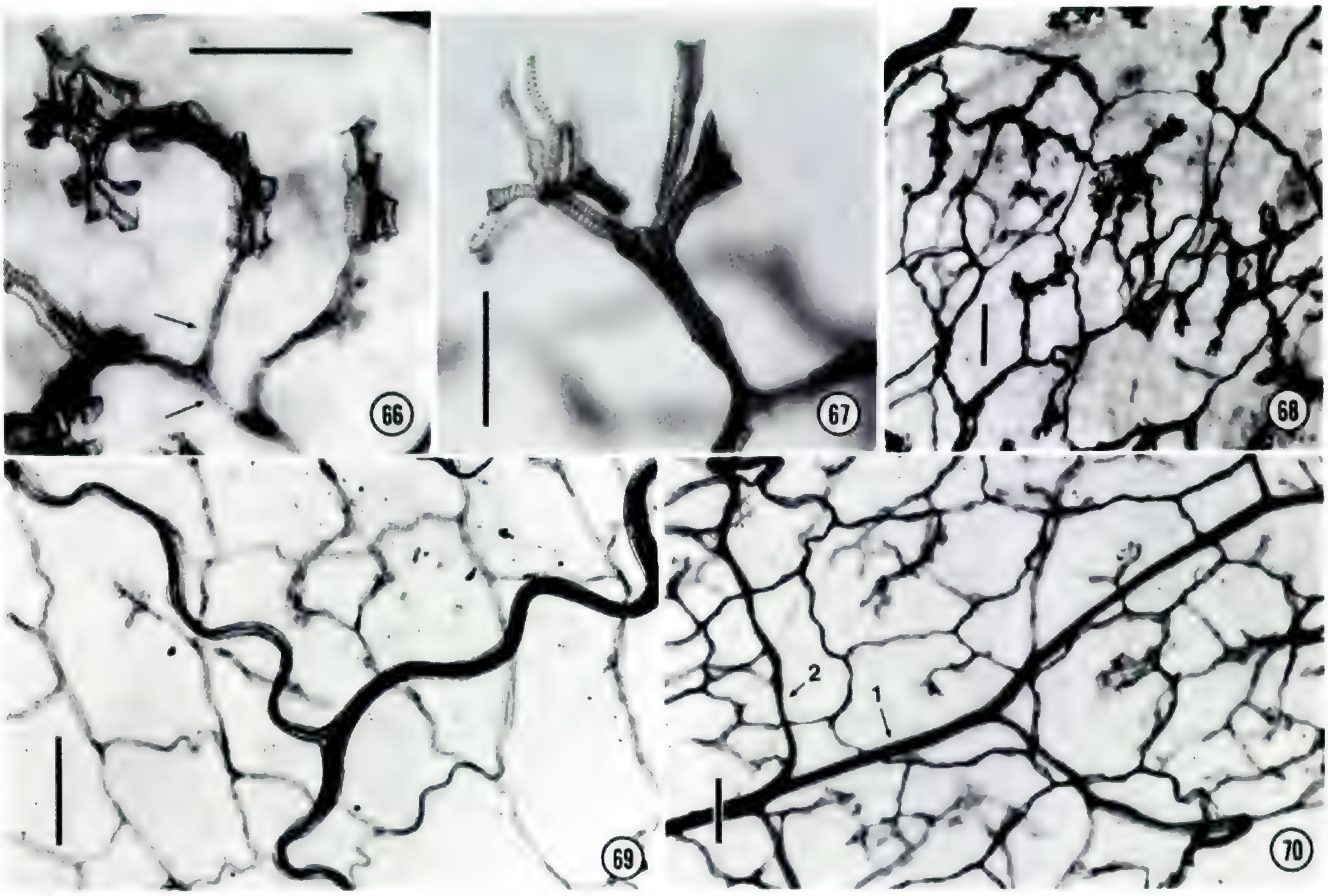




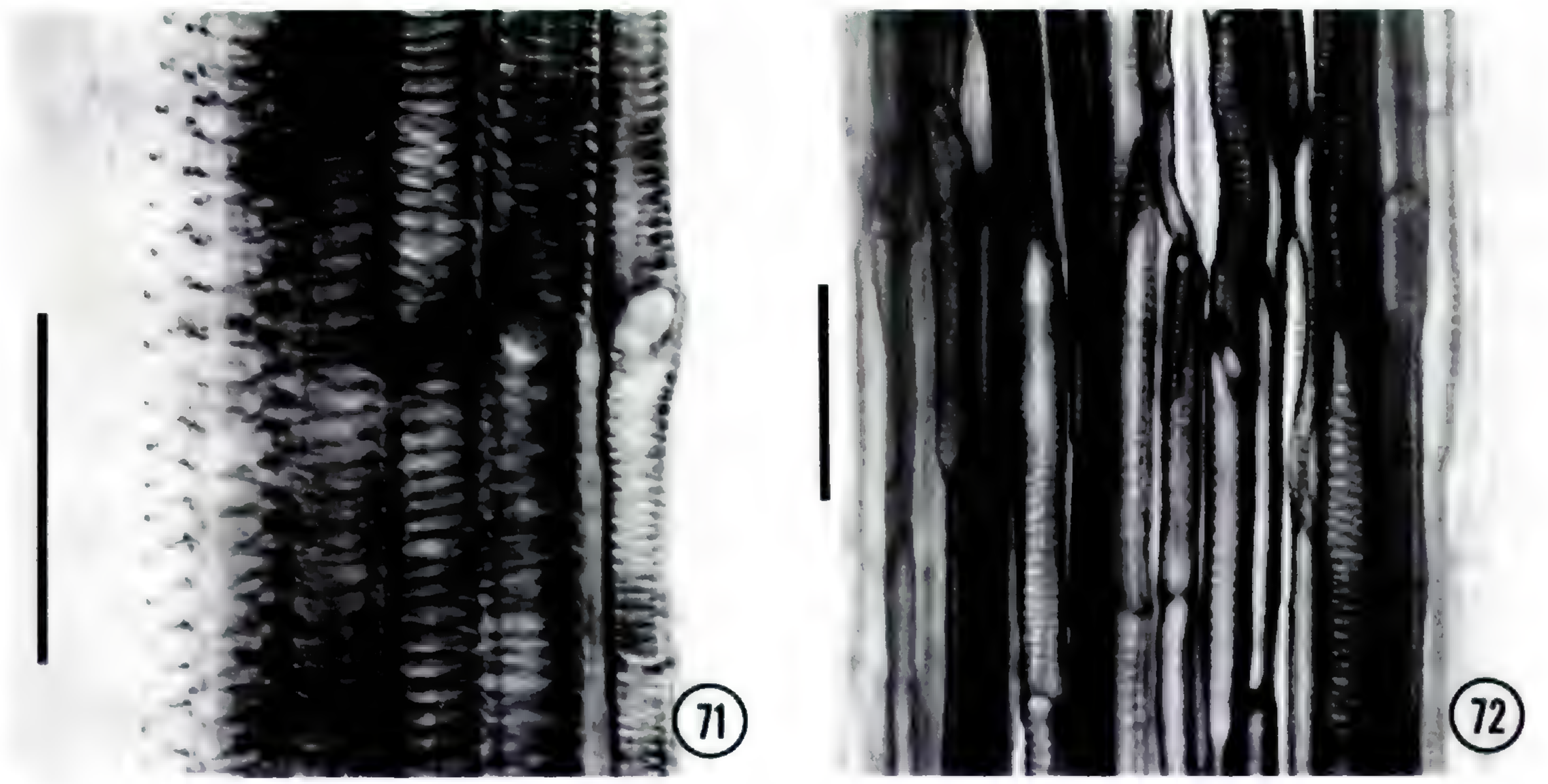




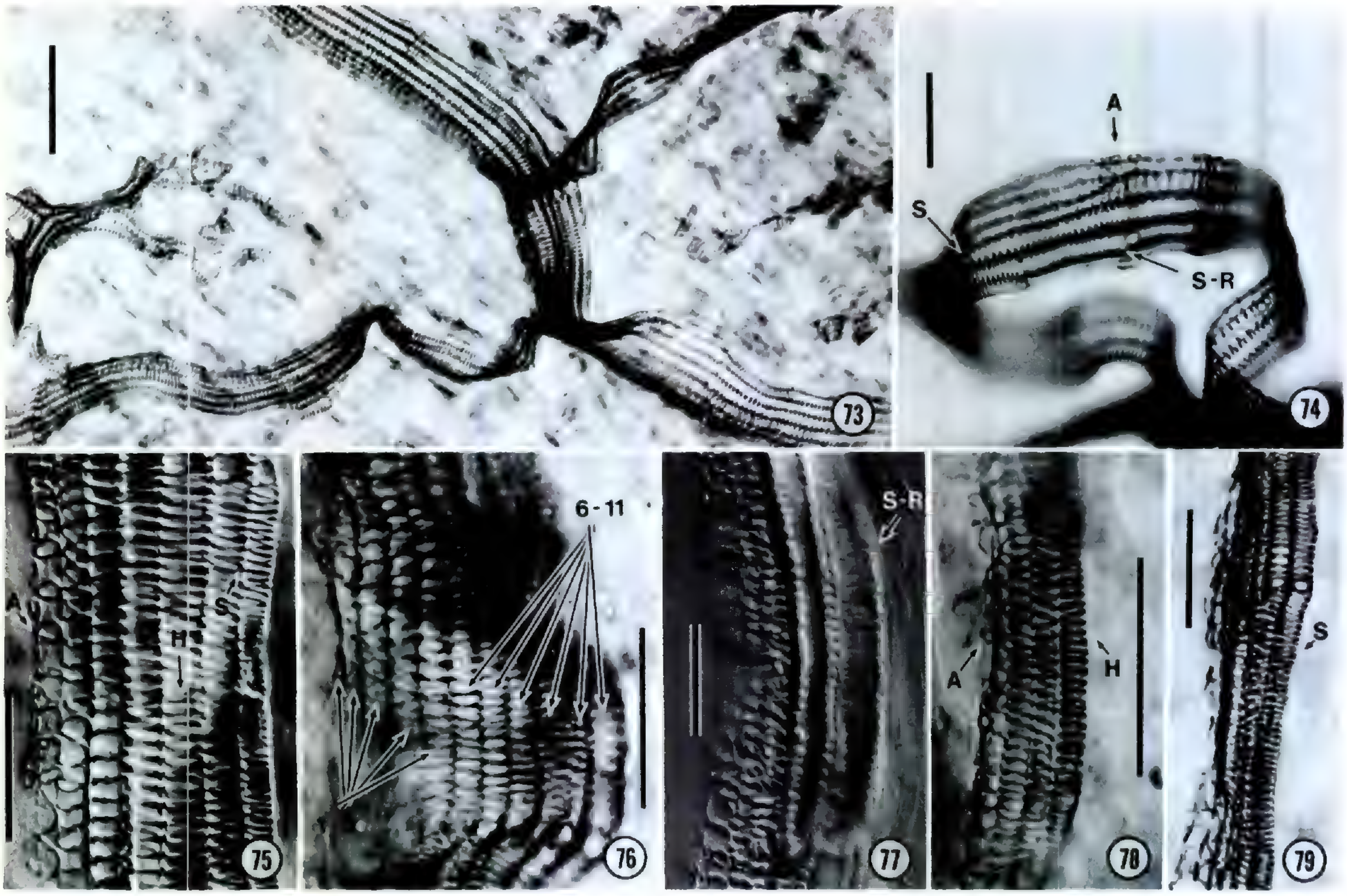
FIGURES 60–65. Fine venation features in *Cistanthe*.—60. Ultimate venation in *C.* (*Calyptridium*) *quadripetala* (*Baker 3075*). Note ribbonlike venation (arrows) and undilated veinlets.—61. Ultimate venation in *C.* (*Calyptridium*) *umbellata* (*Jones 2460*). Note the lack of sinuous veins.—62. Terminal, coalescent veinlets in *C.* (*Cistanthe*) *guadalupensis* (*Wiggins & Ernst 174*).—63. Terminal, coalescent veinlets in *C.* (*Cistanthe*) *grandiflora* (*Werdermann 405*). Note the numerous densely clustered short tracheary elements.—64. Branched veinlet in *C.* (*Cistanthe*) *grandiflora* (*Werdermann 405*). Note the fineness of the vein supplying the dilated veinlet (arrow).—65. Multifurcate, dilated veinlet of *C.* (*Cistanthe*) *picta* var. *picta* (*Pennell 12279*). Scale bars are (μm) 200, 200, 200, 100, 100, and 50, respectively.



FIGURES 66–70. Fine venation features in *Cistanthe*.—66. Dilated veinlets in *C.* (*Cistanthe*) *fenzlii* (*Philippi s.n.*). Note the fineness of the proximal end of the veinlet and the penultimate vein (arrows).—67. Branched veinlet of *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*). Note the lesser degree of veinlet dilation and more elongate terminal tracheary elements relative to other species.—68. Three-dimensional venation in *C.* (*Cistanthe*) *grandiflora* (*Werdermann 405*). The veins reticulate freely in more than one plane.—69. Three-dimensional venation in *C.* (*Cistanthe*) *paniculata* (*Ferreyra 12022*). The plane of focus is on the more prominent, lower-order veins, and the finer, higher-order veins form a reticulum in an adaxial plane.—70. Three-dimensional venation in *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*). The finer, higher-order veins form a reticulum in a plane abaxial to the primary (1) and secondary (2) veins. Scale bars are (μm) 100, 100, 200, 200, and 200, respectively.



FIGURES 71–72. Primary veins of *Cistanthe*.—71. *C.* (*Cistanthe*) *lingulata* (*Lopez 374*) showing helical thickenings of the vessel element walls toward the adaxial side and scalariform to reticulate thickenings toward the abaxial.—72. *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*) showing reticulate thickenings of the vessel element walls. Scale bars = 100 μm.



FIGURES 73–79. Ribbonlike veins in *Cistanthe*.—73. *C.* (*Cistanthe*) *weberbaueri* (*Weberbauer 5321*), showing vein branching, sinuousness of the veins, and a free-ending veinlet (left).—74. *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*) showing sinuousness of the vein.—75. *C.* (*Cistanthe*) *lingulata* (*Lopez 374*).—76. *C.* (*Calyptridium*) *quadripetala* (*Baker 3075*) showing ribbonlike vein 11 tracheary elements wide.—77. *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*) showing scalariform to reticulate vessel element wall thickenings on the abaxial side of the ribbon.—78. *C.* (*Philippiamra*) *celosioides* (*Worth & Morrison 15820*).—79. *C.* (*Cistanthe*) *grandiflora* (*Werdermann 405*). A = annular wall thickenings; H = helical wall thickenings; S = scalariform wall thickenings; S–R = scalariform to reticulate wall thickenings. Scale bars are (μm) 1,000, 50, 50, 50, 50, 50, and 50, respectively.

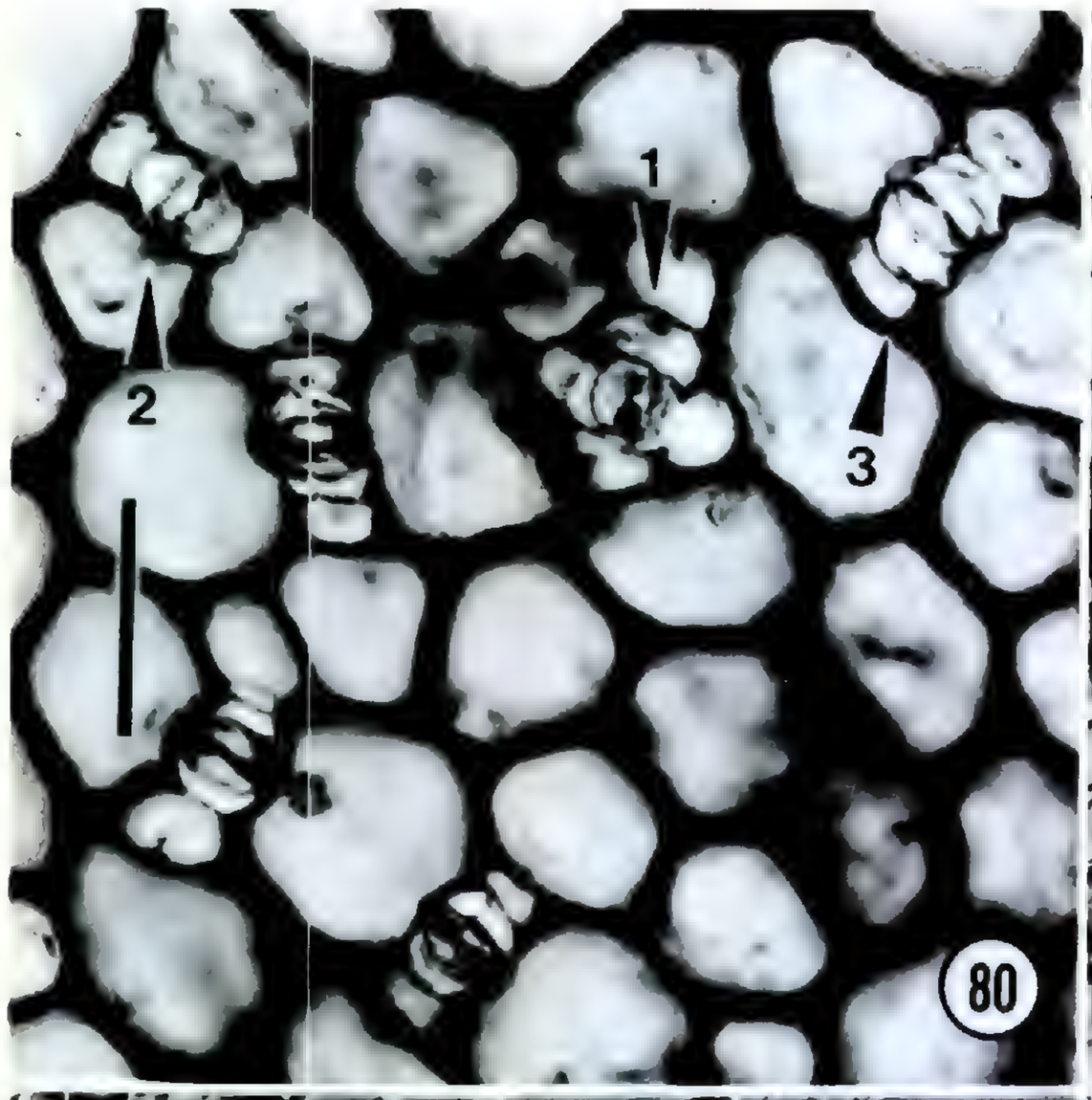
→

FIGURES 80–94. Epidermal morphology in *Cistanthe*. Labels, except where noted, refer to specific features diagrammed in Figure 95 evident in particular stomatal complexes.

FIGURES 80–85. Epidermal morphology in *Cistanthe* sect. *Cistanthe*. All scale bars = ca. 100 μm.—80. *C. grandiflora* (*Werdermann 405*). The plane of focus is subsurface—the stomata are somewhat sunken. 1, more or less hexacytic stoma; 2, hemi-amphibrachyparacytic stoma; 3, amphibrachyparacytic stoma.—81. *C. longiscapa* (*Johnston 5034*). The stomata are slightly sunken. 1, brachyparacytic stoma with four contact cells, cf. Figure 95M and P; 2, amphibrachyparacytic stoma with six contact cells, cf. Figure 95N; 3, similar to 1 above but with five contact cells; 4, more or less brachyparacytic stoma with very broad lateral subsidiary cells; 5, hemibrachyparacytic stoma with three contact cells; 6, stoma with a split lateral subsidiary cell, cf. Figure 95R; 7, amphibrachyparacytic stoma. 82, 83. *C. picta* var. *picta* (*Kuntze s.n.*). —82. 1, brachyparacytic stoma with polygonal subsidiary cells, cf. Figure 95P; 2, hemi-amphibrachyparacytic stoma, cf. Figure 95P and Q; 3, brachyparacytic stoma, cf. Figure 95M and O; 4, brachytetracytic stoma; 5, brachyparacytic stoma, cf. Figure 95I; 6, anomocytic stoma with three contact cells.—83. 1, brachyparacytic stoma, cf. Figure 95I and P; 2, stoma with five contact cells, cf. Figure 95S; 3, stoma with five contact cells, cf. Figure 95R; 4, amphibrachyparacytic stoma; 5, unclassifiable stoma with five contact cells.—84. *C. fenzlii* (*Neger s.n.*). 1, staurocytic stoma with four contact cells, cf. Figure 95G; 2, hemi-amphibrachyparacytic stoma; 3, brachytetracytic stoma; 4, amphibrachyparacytic stoma; 5, stoma with six contact cells but showing essentially the characteristics of Figure 95R.—85. *C. lingulata* (*Ferreyra 10486*). 1, hemi-amphibrachyparacytic stoma; 2, stoma with five contact cells, cf. Figure 95N and R; 3, amphibrachyparacytic stoma, cf. Figure 95K; 4, stoma with five contact cells, cf. Figure 95J and S.

FIGURES 86–90. Epidermal morphology in *Cistanthe* sects. *Cistanthe* and *Amarantoideae*. All scale bars = ca. 100 μm. 86, 87. *C.* (*Cistanthe*) sp. cf. *longiscapa* (*Worth & Morrison 16184*).—86. Epidermal papillae (P).—87. 1, brachyparacytic stoma, cf. Figure 95I and L; 2, hemi-amphibrachyparacytic stoma, cf. Figure 95J and N.—88. *C.* (*Cistanthe*) *cymosa* (*Werdermann 853*). The largest epidermal cells are more or less papillar. The stomata are somewhat sunken. 1, double stoma; 2, hemibrachyparacytic stoma, cf. Figure 95M; 3, anomocytic stoma with four contact cells; 4, brachyparacytic stoma, cf. Figure 95L.—89. *C.* (*Amarantoideae*) *ambigua* (*Nelson & Nelson 3287*). 1, brachyparacytic stoma, cf. Figure 95L and O; 2, stoma with five contact cells, cf. Figure 95L and R; 3, amphibrachyparacytic stoma, cf. Figure 95Q; 4, brachyparacytic stoma, cf. Figure 95L.—90. *C.* (*Amarantoideae*) *salsoloides* (*Werdermann 1048*). 1, amphibrachyparacytic stoma; 2, hemi-amphibrachyparacytic stoma with a polar subsidiary cell, cf. Figure 95T; 3, brachyparacytic stoma with a polar subsidiary cell, cf. Figure 95T.

FIGURES 91–94. Epidermal morphology in *Cistanthe* sects. *Calyptridium* and *Philippiamra*. All scale bars = ca. 100 μm.—91. *C.* (*Calyptridium*) *quadripetala* (*Sharsmith 4345*). 1, brachyparacytic stoma with five contact cells; 2, anomocytic stoma with four contact cells; 3, anomocytic stoma with three contact cells; 4, double stoma; 5, hemibrachyparacytic stoma.—92. *C.* (*Calyptridium*) *umbellata* (*Abrams 11351*). The stomata are slightly to markedly sunken. 1, stoma with five contact cells, cf. Figure 95N and S; 2, brachytetracytic (but nearly hexacytic) stoma, cf. Figure 95E and F; 3, hemi-amphibrachyparacytic stoma with one especially narrow polar subsidiary cell; 4, staurocytic stoma with four contact cells; 5, amphibrachyparacytic stoma.—93. *C.* (*Calyptridium*) *rosea* (*Duran 2805*). The stomata are sunken. 1, anomocytic stoma; 2, hemibrachyparacytic stoma, cf. Figure 95N; P, epidermal papillar cell.—94. *C.* (*Philippiamra*) *celosioides* (*Werdermann 862*). 1, hemi-amphibrachyparacytic stoma (the epidermis is torn on the left side between the subsidiary cell and the guard cell pair); 2, amphibrachyparacytic stoma with five contact cells; 3, amphibrachyparacytic stoma with four contact cells.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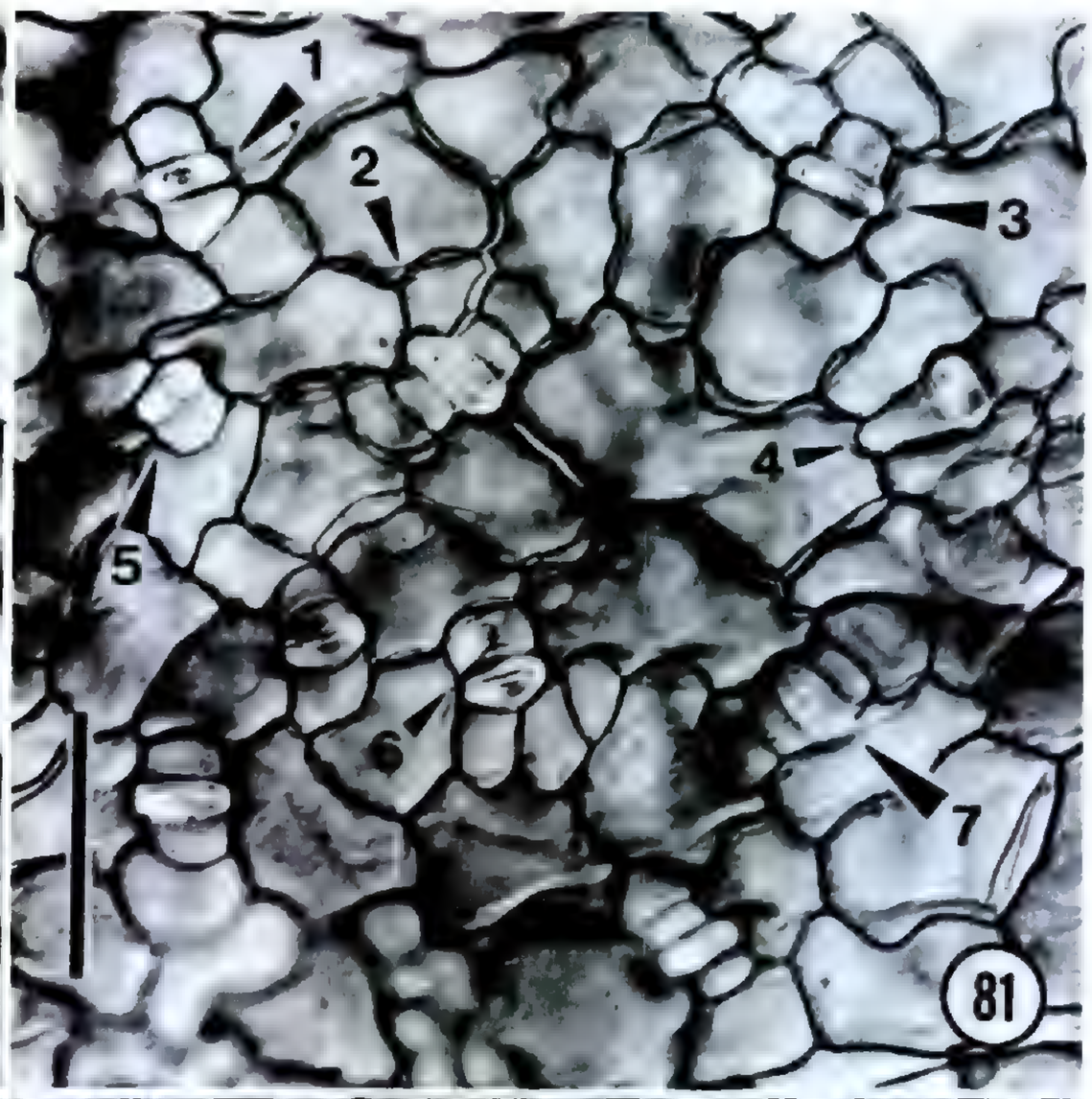
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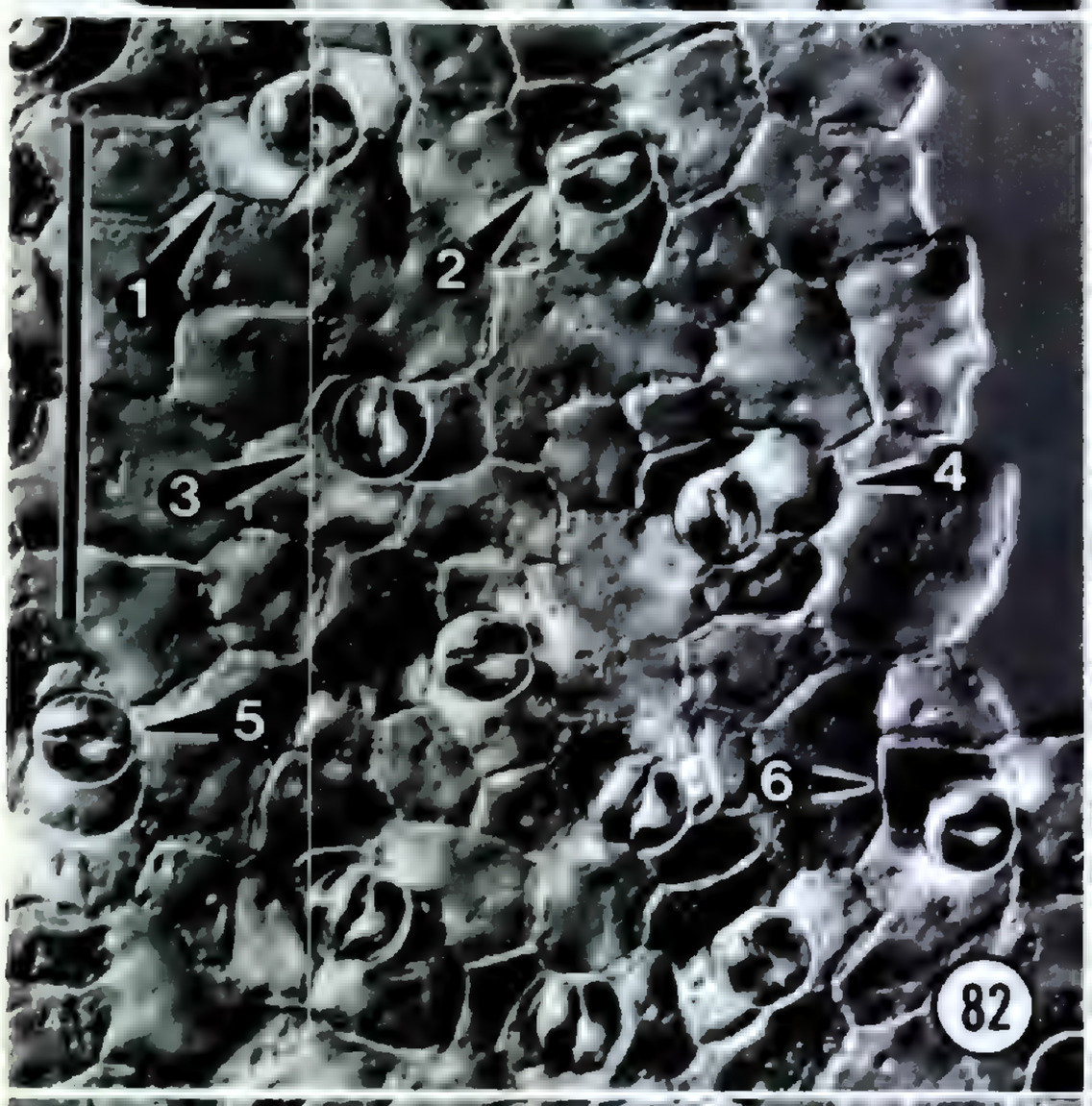
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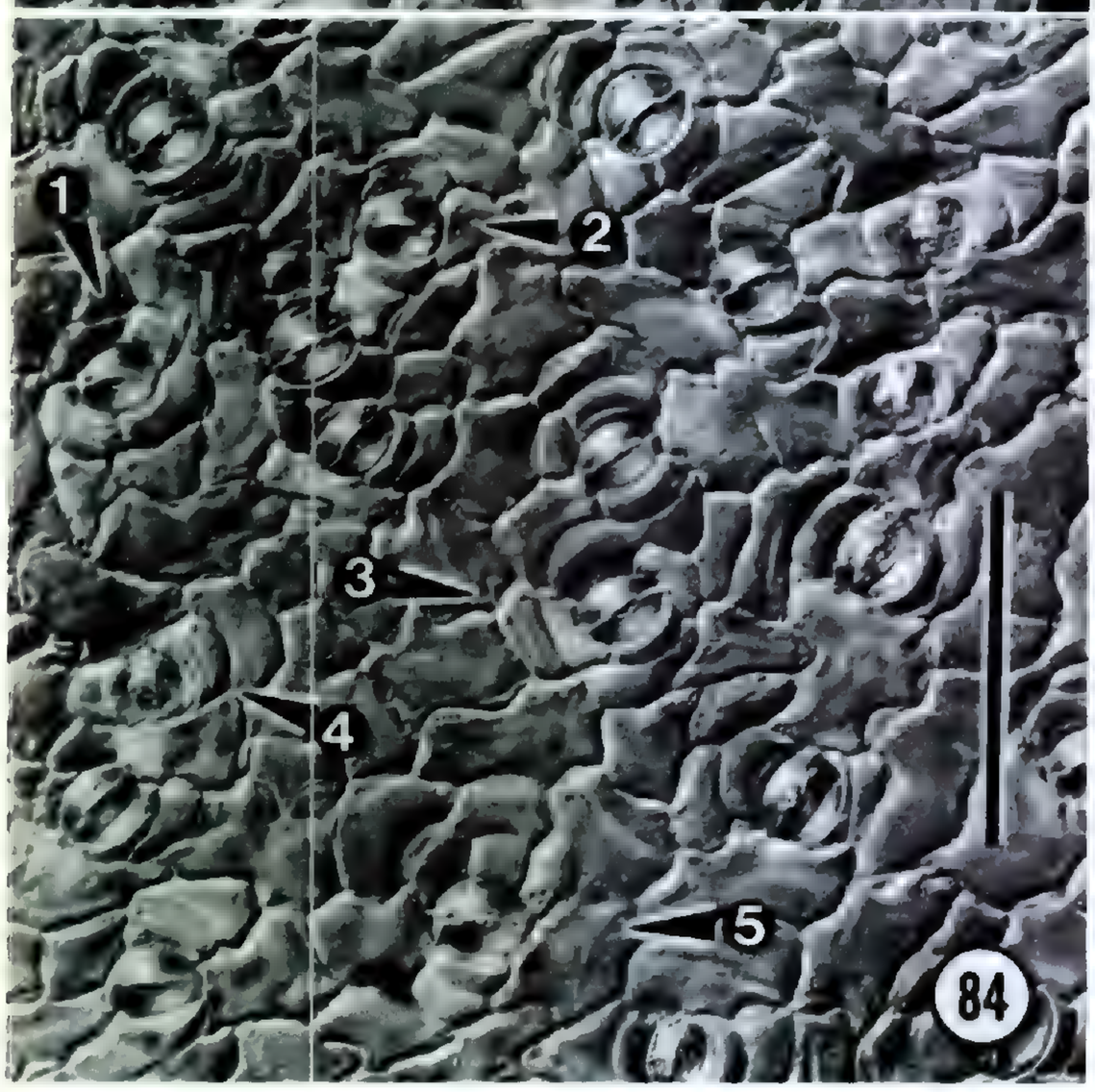
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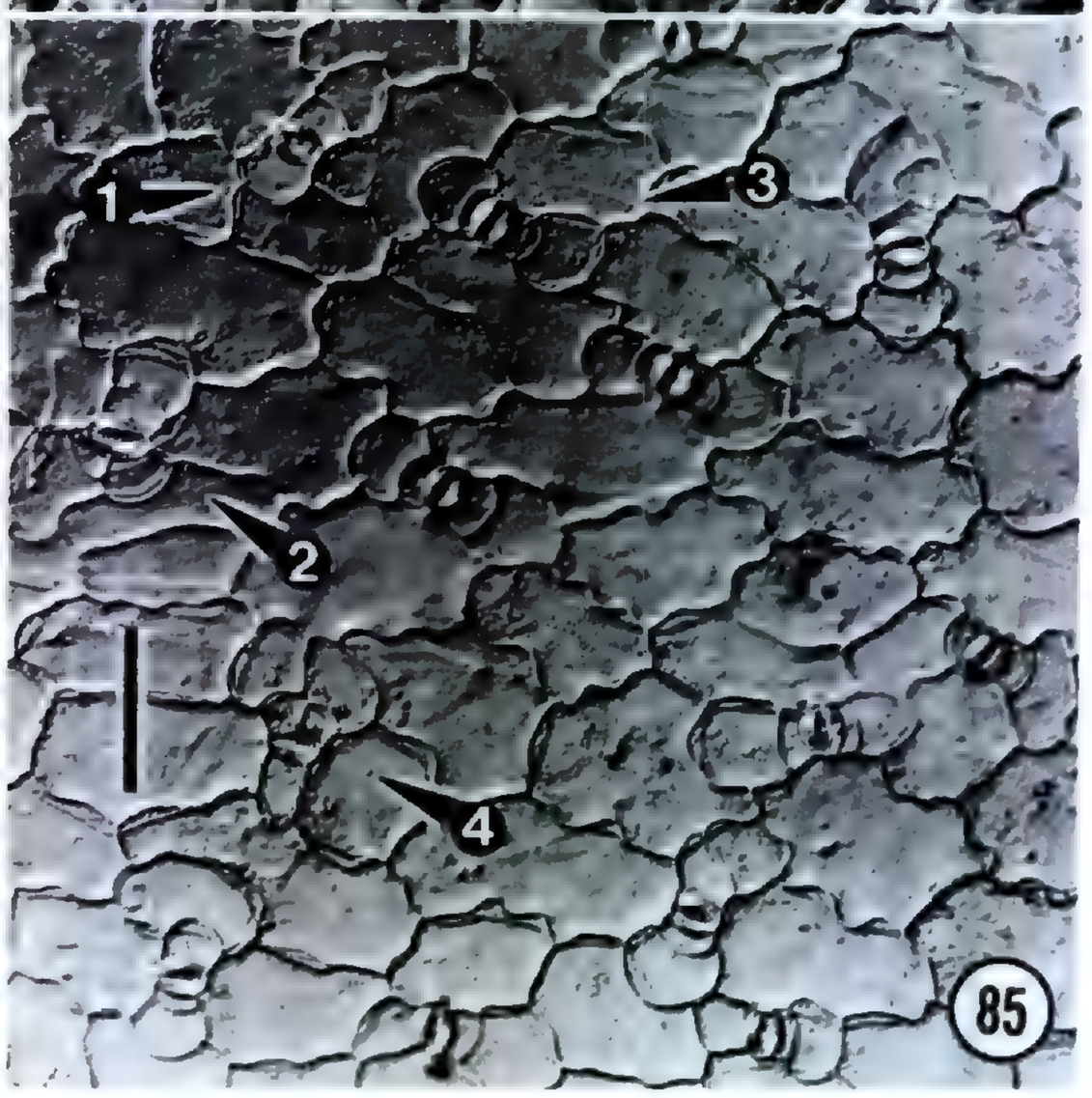
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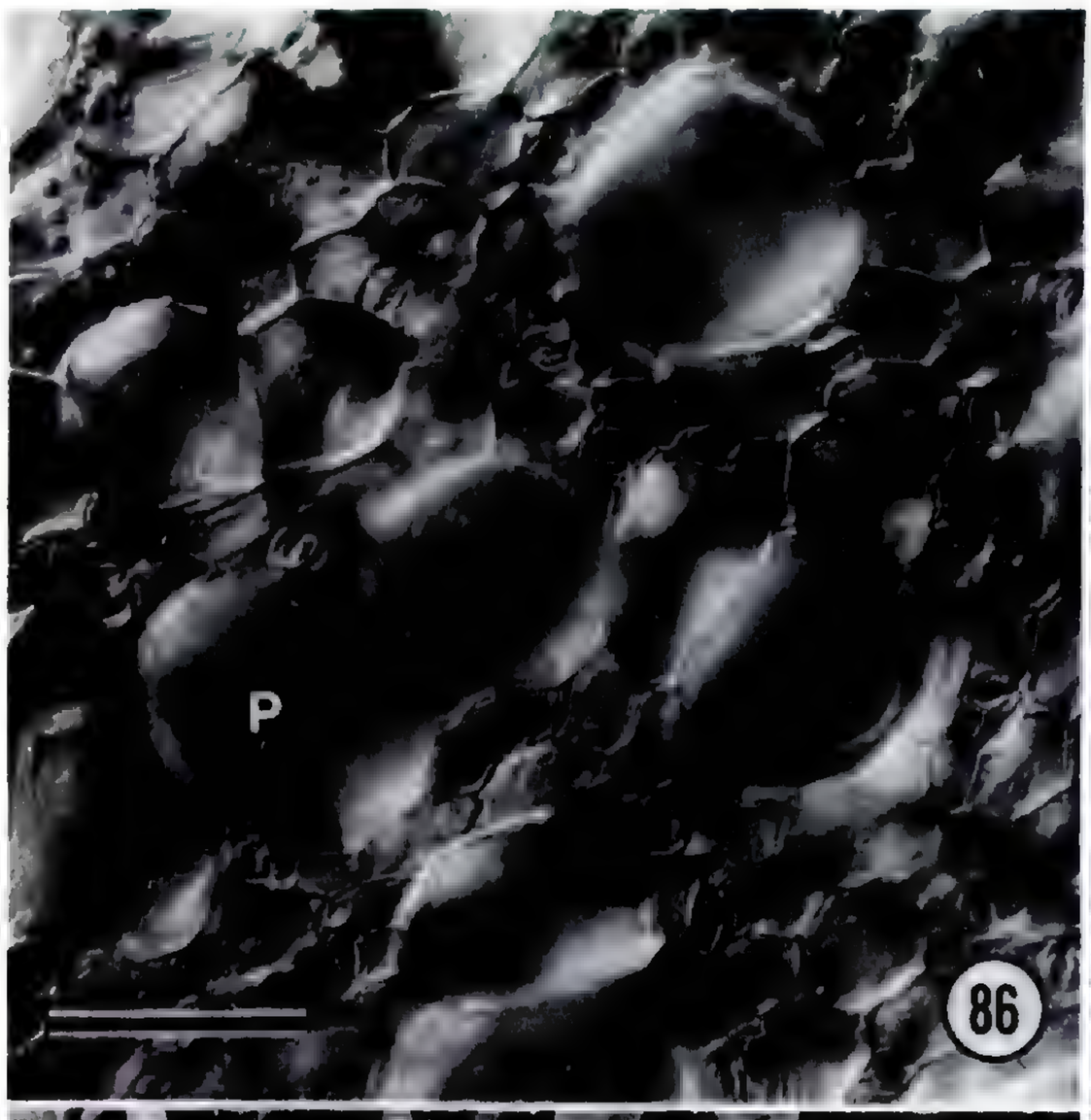
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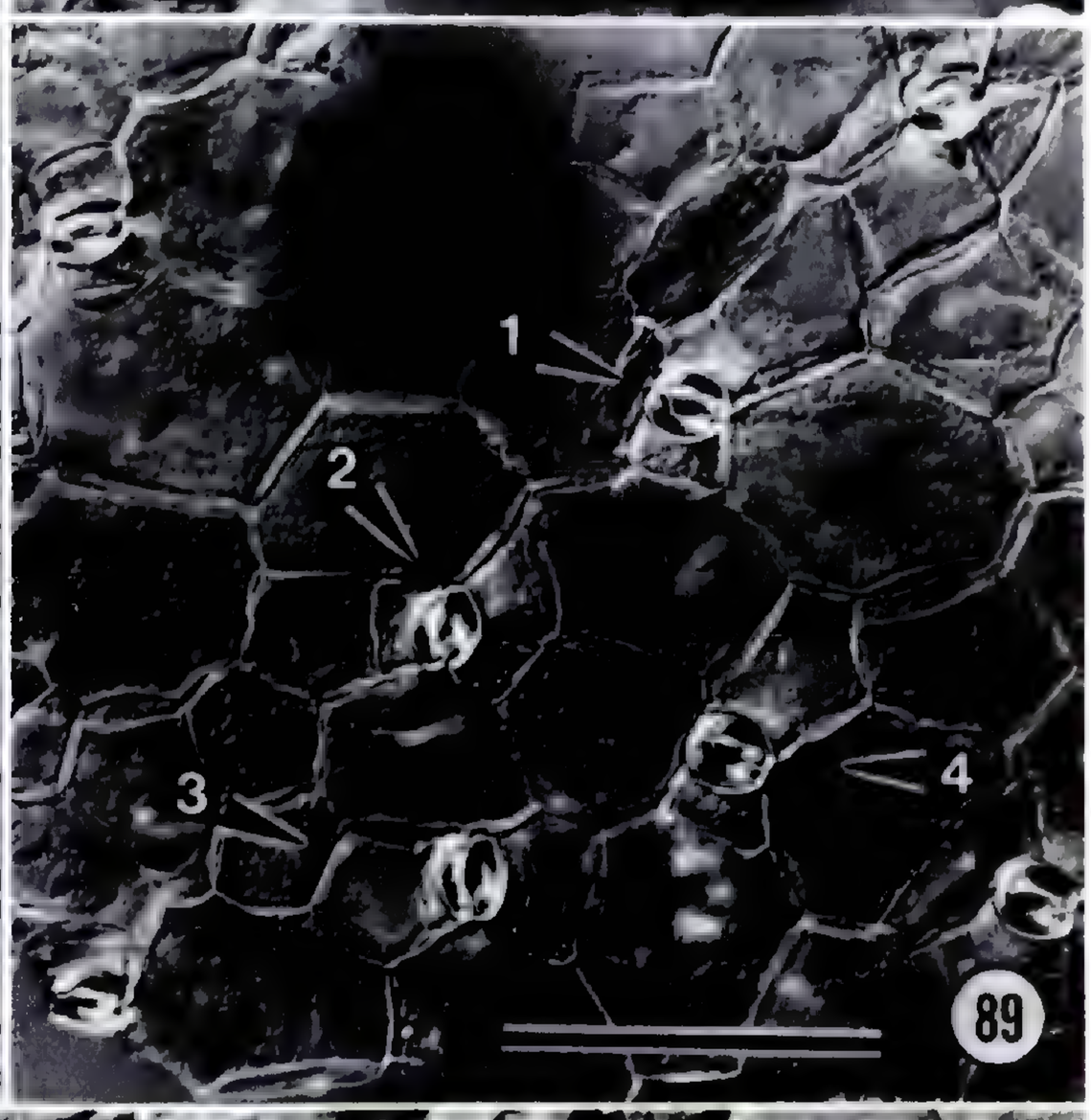
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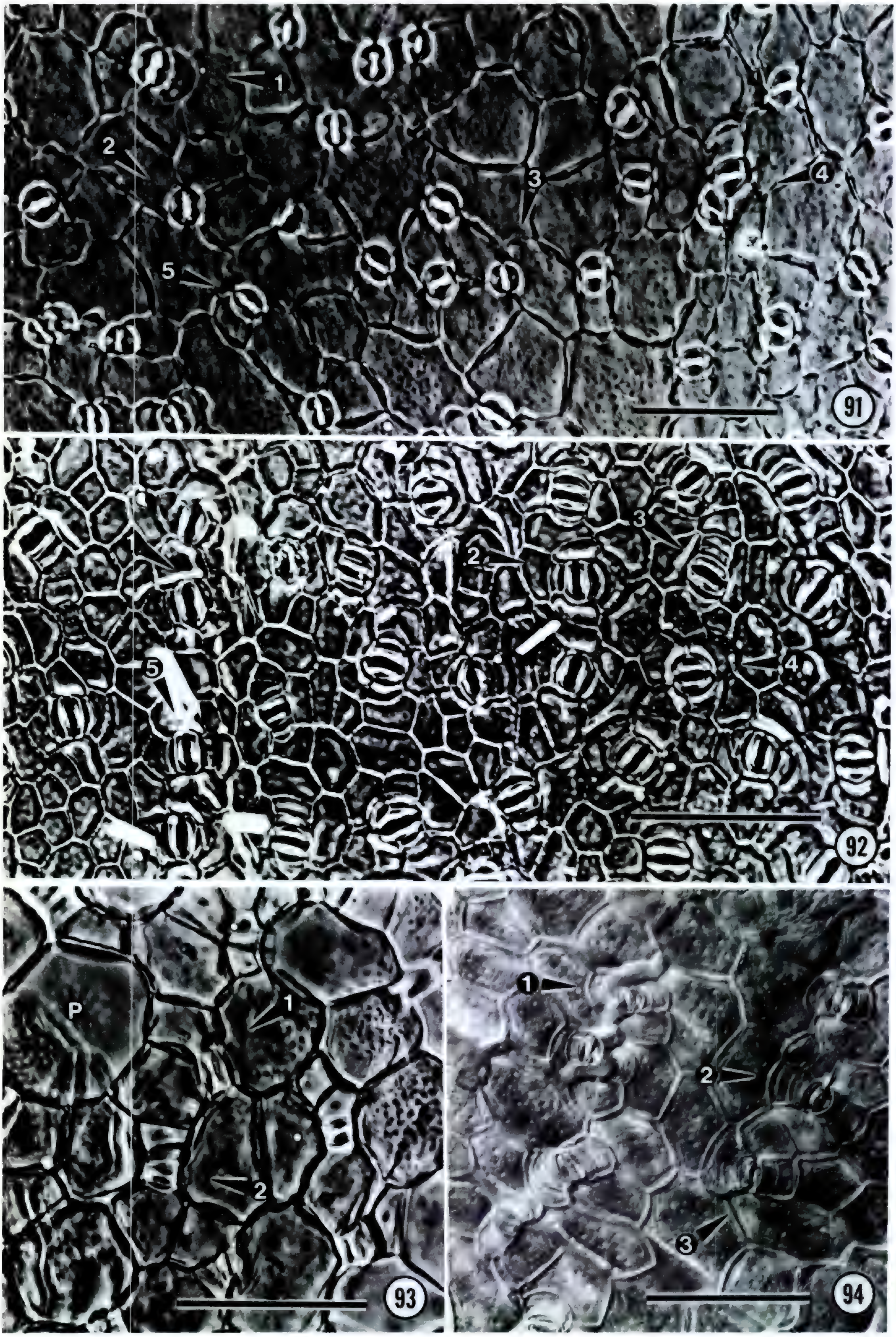
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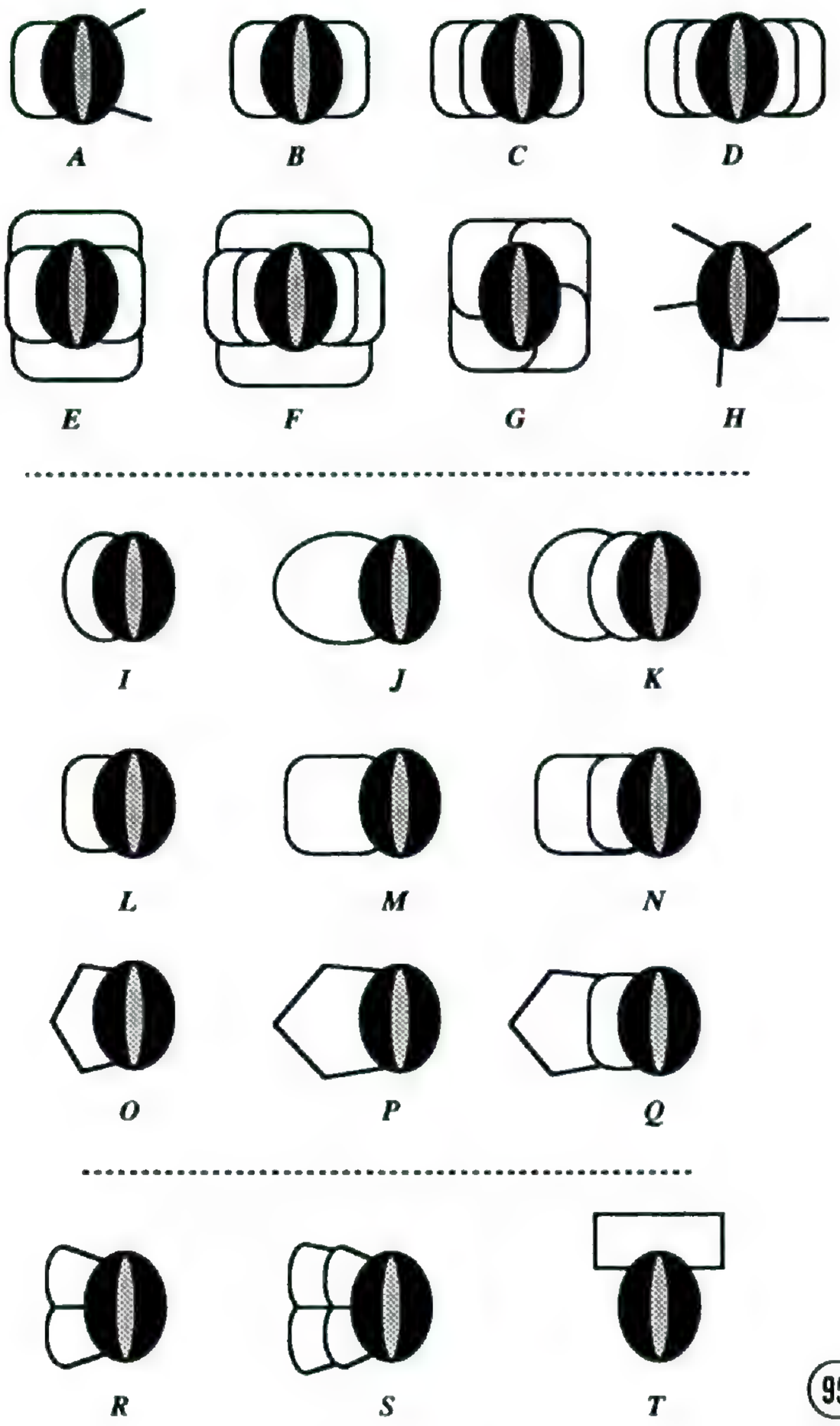

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FIGURE 95. Stomatal complex configurations in *Cistanthe*. A–H, stomatal types, cf. Wilkinson (1979).—A. Hemibrachyparacytic.—B. Brachyparacytic.—C. Hemiamphibrachyparacytic (see text).—D. Amphibrachyparacytic. E. Tetracytic.—F. Hexacytic.—G. Staurocytic.—H. Anomocytic. I–Q. Examples of morphological variation of lateral subsidiary cells.—I. Contoured, narrow.—J. Contoured, broad.—K. Contoured, double.—L. Rectangular, narrow.—M. Rectangular, broad.—N. Rectangular, double.—O. Polygonal, narrow.—P. Polygonal, broad.—Q. Double, the outer polygonal. R–T. Other subsidiary cell types.—R. Lateral cell divided transversely.—S. Two lateral cells, both divided transversely.—T. Polar, elongate cell perpendicular to the guard-cell axis.

PARSIMONY ANALYSIS AND CLADISTIC RECLASSIFICATION OF THE *RELHANIA* GENERIC GROUP (ASTERACEAE–GNAPHALIEAE)

Arne A. Anderberg[1] *and Kåre Bremer*[2]

ABSTRACT

Parsimony analysis of the *Relhania* group of genera (Asteraceae–Gnaphalieae–Relhaniinae) yields a revised hypothesis of their phylogeny. The genera *Leysera* L. and *Oedera* L. are demonstrated to have their closest relatives within *Relhania* L'Hér., which is shown to be paraphyletic as hitherto circumscribed. A revised generic classification is proposed. *Relhania* and *Leysera* are redefined more narrowly. *Rhynchopsidium* DC. and the monotypic *Nestlera* Sprengel are reestablished. *Oedera* is amended to include some former *Relhania* species. The new genus *Comborhiza* Anderb. & Bremer, with 2 species, is described, and 14 new combinations in *Oedera* and *Comborhiza* are made. Because parsimony analysis produces better phylogenetic hypotheses than limited selections of alleged synapomorphies, and because the latter approach hitherto has been more common in generic classification, it is argued that, with improved phylogenetic hypotheses derived from parsimony analysis, generic reclassifications will become necessary also in other groups.

In this paper we present a parsimony analysis and propose a cladistic reclassification of a group of South African Asteraceae genera belonging to the tribe Gnaphalieae. The genera were revised during the 1970s and were then the subjects of some of the first cladistic approaches in botany (Bremer, 1976a, b, 1978a, b). At that time, uniquely derived, qualitative characters that could be interpreted as synapomorphies, unequivocally indicating monophyletic groups were sought. Thus, selected features, mainly of the pappus structure crowning the fruits, were used as putative synapomorphies defining the genera. Today, cladistics is methodologically much more sophisticated and is also considered a standard technique for analyzing phylogenies (Hull, 1989). Application of the parsimony criterion (Farris, 1983) in computerized programs has made it possible to use even large and homoplastic data sets including all kinds of information, minimizing a priori assumptions. Parsimony analysis of the *Relhania* group of genera yields a revised hypothesis of their phylogeny, and hence a basis for a cladistic reclassification.

It is not only the theoretical and methodological background to the study of the phylogeny that has changed during the past 15 years, but also the knowledge of the phylogeny of the tribe Gnaphalieae as a whole (Anderberg, 1991). Furthermore, another genus, not considered in Bremer's 1976–1978 revisions, has recently been added to the group (Anderberg & Källersjö, 1988).

Bremer (1976a, b, 1978a, b) revised the taxonomy and nomenclature of the genera *Relhania*, *Rosenia*, *Leysera*, *Oreoleysera*, and *Antithrixia*. In trying to circumscribe correctly these genera as monophyletic groups, Bremer relied on particular characters as synapomorphies defining them. Thus, *Relhania*, with 29 species, was distinguished by its pappus of more or less connate scales and no bristles. Bremer also pointed out the hypothetical nature of the generic delimitation:

> Admittedly the loss of pappus bristles might have occurred several times. However, since there is no evidence that *Relhania* should be polyphyletic in its present circumscription, I believe we must for the time being rely on this character as uniquely derived and keeping the genus together (Bremer 1976a: 9).

Relhania was amended by Bremer to include most of the species of the genus *Nestlera*, which prior to Bremer's work was used to house all the species with epaleate receptacles. Bremer showed

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that epaleate receptacles were not uniquely derived and could not be used to separate *Nestlera* from *Relhania*. Thus, Bremer (1976b) placed much of *Nestlera* in *Relhania* and transferred some species to *Rosenia*. The latter genus comprises four species and has a pappus of scales as well as 1–4 scabrid bristles.

Later, Bremer (1978a) revised the related genus *Leysera*. It has a pappus of scales and five mostly plumose bristles and was assumed to be monophyletic due to a synapomorphy in the very long peduncles. Again, Bremer commented on the pappus characters used to distinguish the three genera:

> In *Leysera* the disc-floret pappus consists of scales and five (or sometimes fewer) bristles, in *Rosenia* it consists of scales and generally 1–2 bristles, and in *Relhania* there is a disc-floret pappus of scales only. In all three genera there are only scales and no bristles in the ray-floret pappus. These differences are rather slight and the derived conditions might conceivably have been reached more than once but there is no information indicating that the genera should be polyphyletic or paraphyletic. (Bremer 1978a: 371).

Bremer (1978b) also removed one former *Leysera* species with several pappus bristles and described it as the monotypic genus *Oreoleysera*. Another monotypic genus, *Antithrixia*, was noted as a close relative of *Relhania*, *Rosenia*, *Leysera*, and *Oreoleysera*.

Recently, Anderberg & Källersjö (1988) discussed the similarity between *Oedera* and some species of *Relhania*. A transfer of *Oedera*, which comprised six species, from the Anthemideae to the *Relhania* generic group was proposed. In a review of the tribe Gnaphalieae, Anderberg (1991) recognized the subtribe Relhaniinae comprising two major clades, viz. the *Metalasia* group, with 14 genera, and the *Relhania* group, with the genera *Relhania*, *Rosenia*, *Leysera*, *Oreoleysera*, *Antithrixia*, and *Oedera*. Anderberg considered *Oedera* to be the sister group of *Relhania*. However, no synapomorphy could be found to define *Relhania* if *Oedera* was kept separate. Infraspecific relationships between the two genera were not investigated, but the possibility that *Relhania* could be paraphyletic was noted.

Furthermore, Anderberg showed that the monotypic genus *Antithrixia* is the most plesiomorphic representative of the *Relhania* group. The other five genera share a synapomorphy in their pappus scales, absent in *Antithrixia* and the *Metalasia* group. (Bremer, (1978b) erroneously stated that *Oreoleysera* lacks pappus scales, which, albeit very narrow, do exist in *Oreoleysera*).

The presence of a monotypic genus as the sister group of the rest of the *Relhania* group made an analysis of the entire *Relhania* group at the species level conceivable. Based on the characters presented in Tables 1 and 2, we have performed a parsimony analysis of the recognized species of the group, using *Antithrixia* as outgroup. The analysis and its taxonomic implications are presented below.

Methods

DATA

The analysis was based mainly on the characters used by Bremer (1976a, b, 1978a, b) in his revisions. The character list has been amended with further characters by investigating the specimens housed in the Swedish Museum of Natural History (S). The characters are listed in Table 1. Only two species have not been available for study, viz. *Oedera muirii* and *Oedera laevis*. Most of the characters of *Oedera muirii* were possible to extract from the protologue of this species (Smith, 1927), but *Oedera laevis* has been omitted. However, judging from De Candolle's (1838) and Harvey's (1865) descriptions, it seems to be a typical representative of *Oedera*.

ANALYSIS

The data matrix in Table 2 was computed with a parsimony program (Hennig86, version 1.5) written by and obtained from J. S. Farris (1988), and using a standard PC-AT. The following options were used: multiple hennig (mhennig*, constructing several initial cladograms by adding the taxa of the character matrix in several different sequences, retaining the shortest cladogram of each) with a subsequent branch-breaker command (bb*, generating all the multiple, equally parsimonious cladograms that can be found). The cladograms were rooted with a hypothetical ancestor corresponding to the outgroup, *Antithrixia*. The multistate characters 13, 16, 29, and 45 were coded as additive (cc+) because the character states were hypothesized to represent a gradual transformation series. The characters 8, 21, 23, 43, and 46, on the other hand, were coded as nonadditive (cc−), since no such hypothesis could be formulated in these cases.

Results

The analysis resulted in 200 equally parsimonious cladograms, each 123 steps long, with a consistency index (ci) of 0.45. One of these cladograms is shown in Figure 1. The strict consensus

TABLE 1. Characters used in the analysis of the *Relhania*-group. Plesiomorphic states are coded 0 and apomorphic states 1, 2, and 3 with *Antithrixia* as outgroup. See Methods for coding of multistate characters.

1. (0) Perennial half-shrubs or shrubs, (1) annual herbs.
2. (0) Subterranean woody rhizome absent, (1) subterranean woody rhizome present.
3. (0) Stem not subdichotomously branched, (1) stem subdichotomously branched.
4. (0) branches unarmed, (1) branches subspinescent or spinescent.
5. (0) Brachyblasts present, (1) brachyblasts absent.
6. (0) Leaves decussate, (1) leaves alternate.
7. (0) Leaves spreading, (1) leaves squarrose-recurved.
8. (0) Leaves linear–oblong, (1) leaves obovate–spathulate, (2) leaves widely cordate to orbicular.
9. (0) Leaf margin entire, smooth, (1) leaf margin apparently denticulate to sparsely serrate.
10. (0) Leaves blunt, (1) leaves pungent.
11. (0) Leaves mid-nerved, (1) leaves with at least three main nerves.
12. (0) Leaves adaxially more densely pubescent than abaxially, (1) leaves adaxially glabrous.
13. (0) Leaves glandular-hairy with stalked glands, (1) leaves glandular-punctate, (2) leaves glandular-punctate, with glands sunken in pits.
14. (0) Leaf margin not involute, (1) leaf margin involute.
15. (0) Capitula sessile or on short peduncles (generally <25 mm), (1) capitula on long peduncles (generally >25 mm).
16. (0) Capitula solitary, (1) capitula paired to cymose-corymbose or congested, (2) capitula many in dense secondary heads.
17. (0) Synflorescense not surrounded by a leafy involucre, (1) synflorescense surrounded by a leafy involucre.
18. (0) Involucral bracts with spreading limb, (1) involucral bracts with straight limb.
19. (0) At least some involucral bracts spathulate, (1) involucral bracts not spathulate.
20. (0) Receptacle without long squamae, (1) receptacle with long squamae.
21. (0) Receptacle naked, (1) receptacle paleate, with paleae abaxially to the florets, (2) receptacle deeply alveolate.
22. (0) Paleae deciduous, (1) paleae persistent.
23. (0) Paleae entire, (1) paleae apically serrate to laciniate, (2) paleae with two lateral teeth.
24. (0) Ray-florets monomorphic, (1) ray-florets dimorphic.
25. (0) Ray-floret lamina usually 4-veined, (1) ray-floret lamina frequently with up to 10 veins.
26. (0) Ray-floret tube cylindrical, (1) ray-floret tube somewhat triquetrous.
27. (0) Disc-florets perfect, (1) disc-florets functionally male, style undivided.
28. (0) Disc-floret corolla somewhat funnel-shaped, indistinctly divided in tube and limb, (1) disc-floret corolla distinctly divided in tube and limb.

TABLE 1. Continued.

29. (0) Floret tubes eglandular or with few scattered glands, (1) floret tubes regularly glandular, (2) floret tubes with subulate-triangular hairs.
30. (0) Anther appendage acute to obtuse, (1) anther appendage truncate.
31. (0) Anther tails branched, (1) anther tails unbranched.
32. (0) Style branches in disc-florets apically penicillate, truncate, (1) style branches in disc-florets dorsally and apically penicillate, rounded-obtuse.
33. (0) Cypselas oblong-elliptic, (1) cypselas linear.
34. (0) Cypselas of ray-florets terete or angular, (1) cypselas of ray-florets sharply triquetrous.
35. (0) Cypselas of disc-florets terete or angular, (1) cypselas of disc-florets flattened.
36. (0) Cypselas glabrous, (1) cypselas at least in ray-florets pubescent.
37. (0) Cypselas of pubescent ray-florets pilose, (1) cypselas of pubescent ray-florets villose.
38. (0) Cypsela trichomes straight, (1) cypsela trichomes apically coiled.
39. (0) Cypselas generally eglandular, (1) cypselas regularly very glandular.
40. (0) Cypsela epidermis smooth, (1) cypsela epidermis with acute papillae.
41. (0) Cypselas with 5 vascular bundles (occasionally 10), (1) cypselas with 2–3 vascular bundles.
42. (0) Pappus bristles in ray-florets present, (1) pappus bristles in ray-florets absent.
43. (0) Pappus bristles in disc-florets numerous, (1) pappus bristles in disc-florets five, (2) pappus bristles in disc-florets one to four, (3) pappus bristles in disc-florets absent.
44. (0) Pappus bristles apically scabrid to barbellate, (1) pappus bristles apically plumose.
45. (0) Pappus scales free, (1) pappus scales connate, (2) pappus tubular.
46. (0) Basic chromosome number $x = 7$ ($2n = 14, 28, 56$), (1) basic chromosome number $x = 5$ ($2n = 10$), (2) basic chromosome number $x = 4$ ($2n = 8, 16$).

tree in Figure 2 was computed with the nelsen option and shows the clades consistently present in all the equally parsimonious cladograms. In Figures 1 and 2 the terminal taxa are named as in Table 2, following the earlier generic classification, whereas the generic reclassification proposed below is indicated with names in capitals. In the following discussion, *Relhania* s.l., *Leysera* s.l., and *Oedera* s.s. refer to the earlier circumscriptions, whereas *Relhania* s.s., *Leysera* s.s., and *Oedera* s.l. refer to the proposed new delimitations.

Variation among the 200 equally parsimoniously cladograms is restricted to 100 alternative topologies within the screened right part of Figures 1 and 2 (*Oedera* s.l.) as well as to two alternative

TABLE 2. Data matrix. The characters are listed in Table 1. The taxon names follow the earlier classification. Inapplicable, unknown, or variable character states are coded –.

	Character number
	00000000011111111112222222223333333333444444 12345678901234567890123456789012345678901234567890123456
Antithrixia flavicoma	00000000000000000000--0000000000000-0000000--
Oreoleysera montana	00001101000000100010 0--0000010100001000000000-
Leysera longipes	01001100000100100000--00-0110101000--0001100-
Leysera gnaphalodes	0000-10000000001000-10--0000121101001000111102
Leysera tenella	10001100000000100011 0--0000121101001000111102
Leysera leyseroides	10001100000000100111 0--0000121101001000111102
Rosenia glandulosa	00110000000000000010000000000000010000002 01-
Rosenia spinescens	00110000000000000000-0000000000000010000002 01-
Rosenia oppositifolia	00000000000000000000--0000000-0000100000020 10
Rosenia humilis	00-00000000-00000000-0000000000000100000020 10
Relhania dieterlenii	00001000000011000000--0000100100000--00013-1-
Relhania fruticosa	00001100000011000000100000010010000 0--00013-2-
Relhania rotundifolia	00001101000011000000100010010010000 0--00013-2-
Relhania spathulifolia	00001101000011000000000000011001000011000013-10
Relhania corymbosa	00001101000011010000000000010010000110000130 1-
Relhania tricephala	00001101000011010000000000011001000011000013-10
Relhania relhanioides	00001101000011000000000000011001000011000013-1-
Relhania genistifolia	000011-0000110010000100000011010000100-0013-10
Relhania viscosa	00001100000110010000100000011010000100000 13-10
Relhania squarrosa	00001110000110010000100000011010100100000 13-10
Relhania conferta	00001110000110010000100000011010000 0--10113-1-
Relhania steyniae	00001000010110010000100000011010000 0--00013-10
Relhania garnotii	00001110000010010000 2--0001110100001100011 3-10
Relhania multipunctata	00001100000120010100100000011011100 0---0013-1-
Relhania resinifera	00001100000120010110100000011010000100000 13-10
Relhania sedifolia	00001100000120010110100000011 01-10010000013010
Relhania foveolata	00001100000120000000100000010010000100000 13-1-
Relhania nordenstamii	00000000000120010110100000011010000100000 13-1-
Relhania uniflora	00001000000011000000010000001101000010000013-10
Relhania silicicola	00001000000011001000 0--0000110100000--10013-1-
Relhania pumila	10001100000000000010 20-00120100001010011 3-11
Relhania sessiliflora	10001100000000000010102000012010000101001 13-11
Relhania biennis	10001100000000000100--0-00121101001000001 3-21
Relhania tuberosa	01000100000100000000000000011010000100001 13-10
Relhania acerosa	00101100010110000000 0--0000110111001000011 3-1-
Relhania decussata	00001000010010000000110000010011000100001 13-10
Relhania pungens	00001100011000000000110 0-10020010111000011 3-10
Relhania calycina	000011-00111000000001100-10020010111000011 3-10
Relhania speciosa	000011-00111-00000001100110020 0-01110000113-10
Oedera capensis	00001110110100021000101110012010000 0--00013-1-
Oedera hirta	00001112111100021000101110011010000 0--00013-1-
Oedera imbricata	00001112111100021000101110012010000 0--00013-1-
Oedera intermedia	00001110111100021000101110012010000 0--00013-10
Oedera muirii	00001010111100021000101110010010000 0--00-13-1-

sister groups to *Relhania tricephala*, either *R. corymbosa* or the species pair *R. relhanioides* + *R. spathulifolia*, within the screened left part of Figures 1 and 2 (*Relhania* s.s.). The majority of the clades in the cladogram in Figure 1 are present in all the other equally parsimonious cladograms, as shown by the strict consensus tree in Figure 2.

Several analyses were also performed with slight modifications of the data matrix, omitting some characters or including others not accepted in the final matrix (ultimately rejected for various reasons, for example, because of unreliable information in some taxa or because of strong correlation with other included characters such as presence of

FIGURE 1. One of the 200 equally parsimonious cladograms obtained from analysis of the data matrix in Table 2. Black squares = synapomorphies, open squares = synapomorphy with reversals on the cladogram, crosses = reversals, parallel lines = parallelisms. The numbers correspond to the characters in Table 1. Terminal taxon names as in Table 2, following the earlier generic classification in capitals. Proposed new generic classification. Proposed new generic classification in capitals.

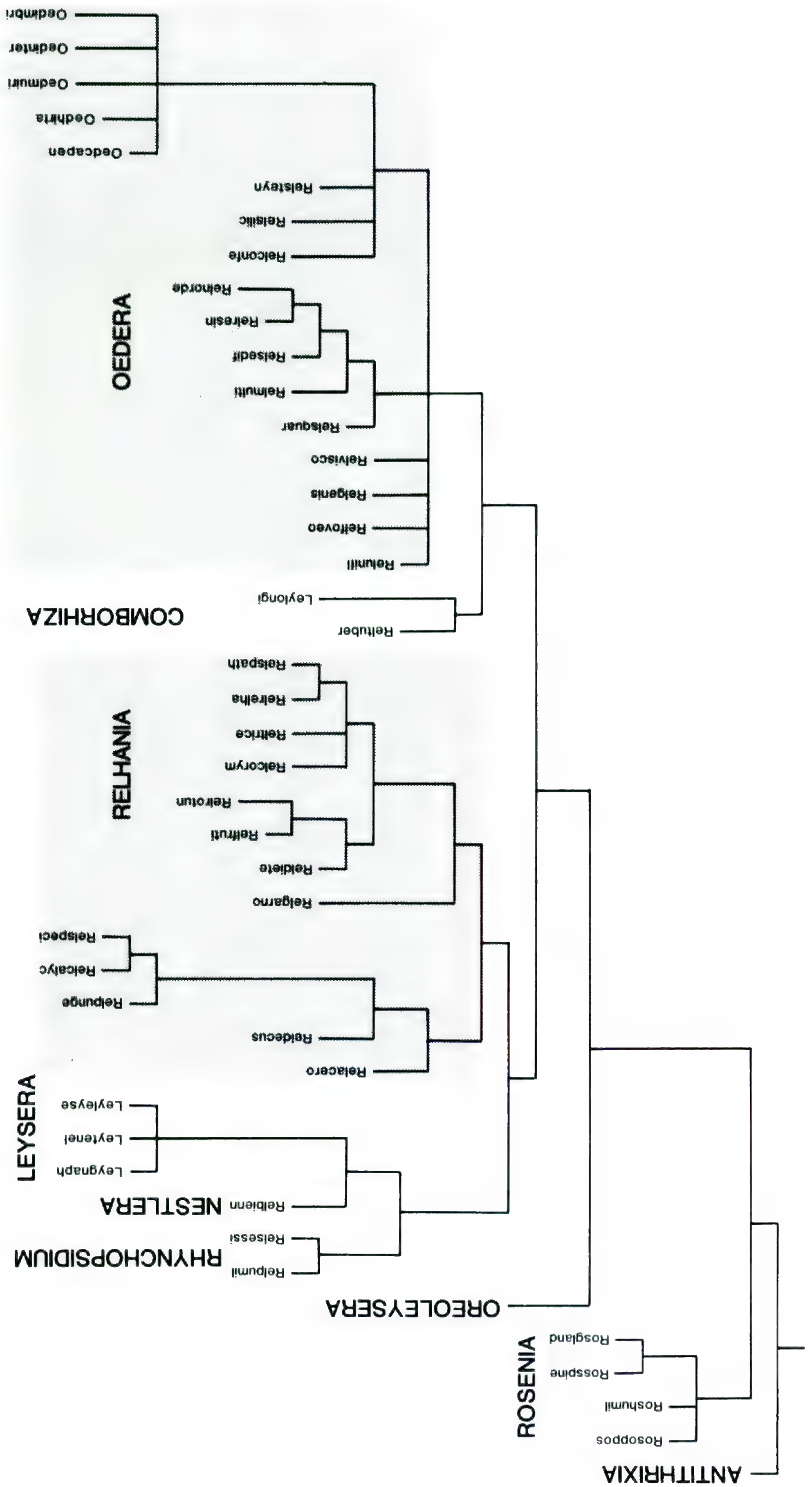

FIGURE 2. Strict consensus tree based on all the 200 equally parsimonious cladograms obtained from analysis of the data matrix in Table 2, following the earlier generic classification. Proposed new generic classification in capitals. Shaded areas show the circumscription of *Relhania* and *Oedera*, respectively.

glands on various organs). These analyses showed, as might be expected, that the clades supported by single parallelisms are weak and easily broken up even with slight changes in the data matrix. However, in all analyses, *Rosenia* and *Oreoleysera* successively came out at the base of the cladogram with the remaining genera as one monophyletic group. Furthermore, *Leysera* and *Oedera* were always firmly nested within a paraphyletic *Relhania* s.l.

Discussion

The consistency index 0.45 and the frequent occurrence of parallelisms and reversals on the cladogram in Figure 1 show that there is considerable homoplasy in the data, as is usually found in similarly sized analyses of other groups. The impact of homoplastic characters on the phylogenetic hypothesis is important, and the most parsimonious way in which these characters can be distributed on a cladogram is virtually impossible to detect without computerized programs. As a scientific theory, the phylogeny reconstructed by parsimony analysis is superior to any phylogeny obtained from a limited selection of characters only, since the former takes into account all available information. Parsimony analysis is increasingly employed in taxonomic revisions, and it offers possibilities for improved, phylogenetically more informative classifications, where the named taxa reflect evolutionary units rather than artificially composed groups defined only by a few characters.

In this case, the analysis clearly demonstrates that *Relhania* s.l. is paraphyletic with *Leysera* and *Oedera* excluded. Delimitation among the three genera has to be altered in order to meet the demand for monophyletic taxa. To lump all genera into a single genus, *Leysera* sensu latissimo (*Leysera* being the oldest name), would result in a very heterogeneous taxon, defined only by characters such as absence of brachyblasts, alternate leaves, glandular floret tube, unbranched anther tails, ray-florets without pappus, and corolla divided in tube and limb. The characters are weak and can, in a wider context, also be shown to be parallelisms (e.g., by investigation of a larger number of taxa of the Gnaphalieae). A better alternative is to split *Relhania* and *Leysera* and recognize smaller monophyletic genera that are more morphologically homogeneous. This would mean the separation of the apomorphic *Leysera* s.s., *Rhynchopsidium*, *Comborhiza*, and *Oedera* from each other, and from *Relhania*. The definition of *Oedera* is hereby weakened due to the transfer to this genus of 10 *Relhania* species. This is unfortunate, but no other alternative is at hand if we want to maintain monophyletic genera. *Relhania* itself is poorly defined but still constitutes a monophyletic group. By accepting this second classification, we gain a detailed, predictive phylogenetic hypothesis with more explanatory power, because more taxonomic statements are made. To reduce all this information of phylogenetic interrelationships and conceal it in a lumping such as outlined above would hardly improve scientific progress.

Consequently, we have resurrected *Nestlera* in its original monotypic sense, reestablished the old ditypic genus *Rhynchopsidium*, described another ditypic genus *Comborhiza*, and transferred a number of the former *Relhania* species to *Oedera* (see Figs. 1, 2).

Relhania is restricted to 13 species, mostly with hairy and glandular-punctate (not glandular-hairy) leaves and solitary capitula. The genus comprises two distinct groups, recognized also by Bremer (1976a), as well as a more isolated species, *R. garnotii*. The two groups are *R. acerosa* to *R. speciosa*, with five species (including the distinct subgroup comprising *R. pungens*, *R. calycina*, and *R. speciosa*), and *R. dieterlenii* to *R. spathulifolia*, with seven species (see Figs. 1, 2).

Leysera is restricted to the three typical species and is thus the most well-defined of all the genera, with a whole set of synapomorphies, e.g., plumose pappus bristles (see Fig. 1). The former *Leysera longipes* and *Relhania tuberosa* are grouped as sister species in the new genus *Comborhiza*. They have a unique synapomorphy in their thick subterranean rhizomes. Although different in several characters, the two species are habitually similar, *Comborhiza virgata* (= *Relhania tuberosa*) having pedunculoid stems with reduced leaves beneath the capitula, approaching the condition in *C. longipes*. The genus has adaxially glabrous, dorsally glandular-hairy leaves, not glandular-punctate as in *Relhania* s.s. and *Oedera* s.l.

The monotypic genus *Nestlera* and the ditypic genus *Rhynchopsidium* are successive sister groups to *Leysera* s.s. (see Figs. 1, 2). Except for the (secondarily) perennial *L. gnaphalodes*, they are annuals or biennials with reduced chromosome base numbers, $x = 5$ in *Rhynchopsidium* and *Nestlera*, and $x = 4$ in *Leysera*. (Humphries et al. (1978) reported $2n = 14$ for *L. leyseroides*, a count that must be doubted in the light of Blanca's (1983) detailed investigation of the karyology of the species; Blanca showed that *L. leyseroides* is a tetraploid with $2n = 16$.)

Oedera, finally, is amended to include 12 former

Relhania species, and as such *Oedera* s.l. is characterized by the generally glabrous, glandular-punctate leaves, and the cymose-corymbose to congested capitula. Infraspecific relationships within *Oedera* are still uncertain. The analysis produced 100 equally parsimonious topologies within *Oedera* s.l. Nevertheless, it must be concluded that *Oedera* s.s. is firmly nested within the larger monophyletic group that we have circumscribed as *Oedera* s.l. Hence, *Oedera* s.s. cannot be maintained at the generic level, since it would leave an unresolved paraphyletic residue of former *Relhania* species.

Conclusion

The former generic classification of the *Relhania* group was based on selected, alleged synapomorphies, the usual cladistic approach during the middle-1970s. Thus, Bremer (1976a, 1978a) defined genera on some pappus features, at the same time pointing out the possibility that the supposed synapomorphies could be false. Parsimony analysis of all the characters has indeed produced a revised picture of the phylogeny. We have recircumscribed genera according to the best phylogenetic hypothesis available, as expressed in the cladograms produced by the analysis. Reclassification of genera like *Relhania* s.l., formerly defined by unique, alleged synapomorphies, which in parsimony analysis of larger groups are shown to be false, is likely to become necessary in many other generic groups as well.

The present classification of the *Relhania* group is summarized in the following key:

1a. Plants compact, cushion-forming ..... *Oreoleysera*
1b. Plants not cushion-forming.
  2a. Pappus of capillary bristles, scales absent ..... *Antithrixia*
  2b. Pappus at least in ray-florets with conspicuous scales, bristles present or absent.
    3a. Pappus bristles distinctly plumose ..... *Leysera*
    3b. Pappus bristles scabrid-barbellate or absent.
      4a. Annual or biennial herbs.
        5a. Cypselas densely hairy with long, apically coiled hairs ..... *Rhynchopsidium*
        5b. Cypselas almost glabrous ..... *Nestlera*
      4b. Perennial half-shrubs, shrublets or shrubs.
        6a. Disc-florets with 1–4 pappus bristles ..... *Rosenia*
        6b. Disc-florets without pappus bristles.
          7a. Plants glabrous (if hairy then with capitula congested in secondary heads), capitula generally cymose-corymbose to clustered in secondary heads (if solitary then with glabrous, ± distinctly one-nerved leaves) ..... *Oedera*
          7b. Plants ± hairy or glandular-hairy (if glabrous then with distinctly 3–9-nerved leaves), capitula generally solitary (if corymbose then with hairy leaves).
            8a. Leaves with long glandular hairs ..... *Comborhiza*
            8b. Leaves without long glandular hairs ..... *Relhania*

Antithrixia DC., Prodr. 6: 277. 1838. TYPE: *A. flavicoma* DC.

Shrublet. *Leaves* opposite or crowded on brachyblasts, sessile, linear, adaxially concave and tomentose, glandular-hairy, apically mucronate; margin entire. *Capitula* solitary, terminal, heterogamous, radiate. Involucral bracts with spathulate laminas. *Receptacle* flat, epaleate. *Female florets* yellow with purple bands dorsally, pistillate, radiate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow. Anthers ecalcarate with short tails; endothecial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping-hairs apically. *Cypselas* rodlike, with ten (2 × 5) vascular bundles, glabrous or with a few scattered, elongated twin hairs. Pappus of slightly connate, barbellate, capillary bristles in one to two rows. *Chromosome number* unknown.

Monotypic: *A. flavicoma* DC. Reference: Bremer, 1978b.

Rosenia Thunb., Nov. Gen. 161. 1800. TYPE: *R. glandulosa* Thunb.

Synonym: *Polychaetia* Less.

Shrublets. *Leaves* decussate or rarely alternate, straight, adaxially concave, tomentose, glandular-hairy; margin entire. *Capitula* heterogamous, radiate, solitary or few together. Involucral bracts with spathulate laminas. *Receptacle* flat, often paleate. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets.

Disc-florets perfect. Corolla yellow. Anthers ecalcarate with short tails; endothecial tissue polarized; apical appendage acute. Style branches ± truncate with obtuse sweeping-hairs apically. *Cypselas* rodlike with five vascular bundles, sparsely hairy with elongated twin hairs. Pappus a crown of ± free scales, and 1–4, barbellate, capillary bristles with flattened apical portion. *Chromosome number* $2n = 14, 28, 56$.

Four species: *R. glandulosa* Thunb., *R. humilis* (Less.) Bremer, *R. oppositifolia* (DC.) Bremer, *R. spinescens* DC. Reference: Bremer, 1976b.

Oreoleysera Bremer, Bot. Not. 131: 450. 1978. TYPE: *O. montana* (Bolus) Bremer.

Compact woody perennial, forming dense tufts. *Leaves* alternate, sessile, narrowly oblong, flattened, grayish tomentose on both surfaces, eglandular; margin entire. *Capitula* solitary, terminal on long leafless peduncles, heterogamous, radiate. Involucral bracts with lanceolate laminas. *Receptacle* flat, epaleate. *Female florets* yellow with purple bands dorsally, pistillate, radiate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow, glandular-hairy. Anthers ecalcarate with short tails; endothecial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping hairs apically. *Cypselas* rodlike with five vascular bundles, moderately hairy with elongated twin hairs. Pappus of free, barbellate, capillary bristles in one row with an outer row of very narrow scales. *Chromosome number* unknown.

Monotypic: *O. montana* (Bolus) Bremer. Reference: Bremer, 1978b.

Rhynchopsidium DC., Mém. Soc. Phys. Genève 7: 283. 1836. TYPE: *R. sessiliflorum* (L. f.) DC.

Synonym: *Rhynchocarpus* Less., nom. illeg.

Annual herbs. *Leaves* alternate or sometimes opposite, straight, adaxially concave, tomentose, glandular-hairy; margin entire. *Capitula* heterogamous, radiate, solitary, sessile or pedunculate. Involucral bracts with lanceolate laminas. *Receptacle* flat–convex, paleate; paleae lanceolate with two lateral teeth. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow, often with robust multicellular trichomes. Anthers ecalcarate, with short tails; endothecial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping-hairs apically. *Cypselas* narrowly elliptic with three vascular bundles, densely hairy with elongated, apically coiled twin hairs. Pappus a crown of ± free scales. *Chromosome number* $2n = 10$.

Two species: *R. pumilum* (L. f.) DC. (= *Relhania pumila* (L. f.) Thunb.), *R. sessiliflorum* (L. f.) DC. (= *Relhania sessiflora* (L. f.) Thunb.). Reference: Bremer 1976a (spp. 21–22).

Nestlera Sprengel, Anleit. Kennt. Gewächse 2(2): 568. 1818. TYPE: *N. biennis* (Jacq.) Sprengel.

Synonyms: *Columellea* Jacq. nom. illeg., *Stephanopappus* Less.

Biennial herb. *Leaves* alternate or occasionally opposite, straight, adaxially concave, tomentose, glandular-hairy; glands with multicellular heads; margin entire. *Capitula* heterogamous, radiate, solitary or few together. Involucral bracts with lanceolate laminas. *Receptacle* flat, often paleate. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow, often with robust multicellular trichomes. Anthers ecalcarate, with short tails; endothecial tissue polarized; apical appendage truncate. Style-branches ± truncate with obtuse sweeping-hairs apically. *Cypselas* rodlike with five vascular bundles, sparsely hairy with elongated twin hairs. Pappus a tubular crown of connate scales. *Chromosome number* $2n = 10$.

Monotypic: *N. biennis* (Jacq.) Sprengel (= *Relhania biennis* (Jacq.) Bremer). Reference: Bremer, 1976a (sp. 23).

Leysera L. Sp. Pl. ed. 2, 2: 1249, 1763; Amoen. Acad. 6: 104, 1763; Gen. Pl. ed. 6: 431, 1764. TYPE: *L. gnaphalodes* (L.) L.

Synonyms: *Asteropterus* (Vaill.) Adans., *Callicornia* Burm. f., *Callisia* L., *Leptophytus* Cass., *Longchampia* Willd., *Pseudocrupina* Velen., *Leyseria* Necker, *Leyssera* auct., ortogr. var.

Annual herbs or a perennial half-shrub or shrublet. *Leaves* alternate or occasionally opposite, sessile, linear, straight, mucronate, adaxially concave, tomentose, glandular-hairy; margin entire. *Capitula* heterogamous, radiate, solitary, terminal on long leafless peduncles. Involucral bracts with lanceolate laminas. *Receptacle* flat, marginally with prominent squamae. *Female florets* yellow with

purple bands dorsally, radiate or miniradiate, pistillate, in one row, fewer than the disc-florets; tube often with robust, conical trichomes. *Cypselas* as in disc-florets. Pappus of scales only. *Disc-florets* perfect. Corolla yellow, often with robust multicellular trichomes. Anthers ecalcarate, with short tails; endothecial tissue polarized; apical appendage truncate. Style branches truncate with obtuse sweeping-hairs apically. *Cypselas* rodlike, with three vascular bundles, glabrous or with scattered, elongated twin hairs. Pappus of free, apically plumose, capillary bristles in one row with an outer row of obtuse scales. *Chromosome number* $2n = 8, 16$.

Three species: *L. gnaphalodes* (L.) L., *L. leyseroides* (Desf.) Maire, *L. tenella* DC. Reference: Bremer, 1978a.

Relhania L'Hér., nom. cons.. Sert. Angl. 1: 22, 1789. TYPE: *R. fruticosa* (L.) Bremer.

Synonyms: *Osmites* L., *Lapeirousia* Thunb., nom. illeg.

Shrubs, shrublets, or half-shrubs. *Leaves* alternate or decussate, sessile, straight, adaxially concave, tomentose, margin entire. *Capitula* heterogamous, radiate, solitary or sometimes cymose-corymbose. Involucral bracts with spathulate laminas. *Receptacle* flat to convex or rarely deeply alveolate, often paleate. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect or functionally male. Corolla yellow, sometimes with robust multicellular trichomes. Anthers ecalcarate, with short tails; endothecial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping-hairs apically (rarely obtuse with sweeping-hairs dorsally). *Cypselas* rodlike with 5 or 3 vascular bundles, glabrous or sparsely hairy with elongated twin hairs. Pappus a crown of free to connate scales without bristles, occasionally with 1 or 2 barbellate bristles in odd florets. *Chromosome number* $2n = 14$.

Thirteen species: *R. acerosa* (DC.) Bremer, *R. calycina* (L. f.) L'Hér., *R. corymbosa* (Bolus) Bremer, *R. decussata* L'Hér., *R. dieterlenii* (E. Phillips) Bremer, *R. fruticosa* (L.) Bremer, *R. garnotii* (Less.) Bremer, *R. pungens* L'Hér., *R. relhanioides* (Schltr.) Bremer, *R. rotundifolia* Less., *R. spathulifolia* Bremer, *R. speciosa* (DC.) Harv., *R. tricephala* (DC.) Bremer. Reference: Bremer, 1976a (spp. 1–7, 13, 25–29).

Comborhiza Anderb. & Bremer, gen. nov. TYPE: *C. virgata* (N. E. Br.) Anderb. & Bremer. Eponymy: The name is deduced from the Greek words *combos*, meaning knot, tuber, and *rhiza*, meaning root.

Fruticulus vel suffrutex. Caules rhizomate vel tubere hypogaeo, crasso, lignoso exorientes. *Folia* alterna vel in brachyblastis congesta, sessilia, stricta, concava, inferne glandulis longistipitatis praedita, superne glabra, margine integra. *Capitula* heterogama, radiata, solitaria, ad apices caulium paucifoliatorum vel pedunculorum longissimorum. Bracteae involucri pluriseriatae lamina scariosa, spathulata infuscata. *Receptaculum* planum vel convexum, epaleatum. *Flosculi radii* flavi sed dorso interdum purpureo-fasciati, pistillati, uniseriati, flosculos disci pauciores. *Cypselae* eaedem in flosculis disci. Pappus ex squamis angustis scariosis constans. *Flosculi disci* perfecti. Corolla flava. Antherae ecalcaratae, breviter caudatae, appendicibus apicalibus acutis; endothecio polarato. Styli rami apice truncati, pilis obtusis apicaliter. *Cypselae* anguste ellipticae, tri- vel quinquevenosae, pilosae vel fere glabrae. Pappus ex setis liberis, capillaribus, barbellatis, uniseriatis et squamis angustis scariosis vel tantum squamis scariosis plus minusve connatis solum constans.

Shrublet or suffrutex. Stems arising from subterranean, thick woody tubers or rhizomes. *Leaves* alternate or crowded on brachyblasts, sessile, straight, adaxially concave, glabrous above, glandular-hairy below, margin entire. *Capitula* heterogamous, radiate, solitary, on pedunculoid few-leaved stems or on long leafless peduncles. Involucral bracts with spathulate laminas. *Receptacle* flat or flat to convex, epaleate. *Female florets* yellow with purple bands dorsally, radiate, pistillate, in one row, fewer than the disc-florets. *Cypselas* as in disc-florets. Pappus of narrow scales. *Disc-florets* perfect. Corolla yellow. Anthers ecalcarate, with short tails; endothecial tissue polarized; apical appendage acute. Style branches truncate with obtuse sweeping-hairs apically. *Cypselas* narrowly elliptic with five or three vascular bundles, glabrous or sparsely hairy with elongated twin hairs. Pappus of 5 barbellate capillary bristles and narrow scales, or of ± connate scales only. *Chromosome number* $2n = 14$.

Two species:

C. longipes (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Leysera longipes* Bremer, Bot. Not. 131: 381. 1978.

C. virgata (N. E. Br.) Anderb. & Bremer, comb. nov. Basionym: *Nestlera virgata* N. E. Br., Kew Bull. 1895: 25 (= *Relhania tuberosa* Bremer).

References: Bremer, 1976a (sp. 24), 1978a (sp. 4).

Oedera L., nom. cons. emend. Anderb. & Bremer, emend nov. Mant. Pl. 159, 1771. TYPE: *O. capensis* (L.) Druce.

Synonyms: *Eroeda* Levyns, nom. illeg., *Eclopes* Gaertner.

Shrubs or shrublets. *Leaves* alternate or decussate, ovate to linear, mucronate, adaxially concave, glabrous or sometimes sparsely pilose, glandular; margin entire but sometimes provided with prominent, robust teethlike hairs. *Capitula* generally densely cymose-corymbose or even forming secondary heads surrounded by a common involucre of leaves, heterogamous, radiate, few-flowered. Involucral bracts with spathulate laminas. *Receptacle* flat to conical-convex, paleate or occasionally epaleate. *Female florets* yellow with purple bands dorsally, radiate in some species miniradiate or almost tubular in different positions in the head, in one row, fewer than the disc-florets. *Cypselas* and pappus as in disc-florets. *Disc-florets* perfect. Corolla yellow, sometimes with robust multicellular trichomes. Anthers ecalcarate, with short tails; endothecial tissue polarized; apical appendage acute. Style branches generally truncate with obtuse sweeping-hairs apically. *Cypselas* rodlike, with 5 vascular bundles, glabrous or with a few elongated twin hairs. Pappus a crown of ± connate scales, without bristles. *Chromosome number* $2n = 14$.

Eighteen species:

O. capensis (L.) Druce, *O. hirta* Thunb., *O. imbricata* Lam., *O. intermedia* DC., *O. laevis* DC., *O. muirii* C. A. Smith.

O. conferta (Hutch.) Anderb. & Bremer comb. nov. Basionym: *Relhania conferta* Hutch., Ann. S. African Mus. 9: 381. 1917.

O. foveolata (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Relhania foveolata* Bremer, Opera Bot. 40: 52. 1976.

O. genistifolia (L.) Anderb. & Bremer, comb. nov. Basionym: *Athanasia genistifolia* L., Syst. Nat. 2 Ed. 12: 540. 1767 (= *Relhania genistifolia* (L.) L'Hér.).

O. multipunctata (DC.) Anderb. & Bremer, comb. nov. Basionym: *Relhania multipunctata* DC., Prodr. 6: 286, 1838.

O. nordenstamii (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Relhania nordenstamii* Bremer, Opera Bot. 40: 54, 1976.

O. resinifera (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Relhania resinifera* Bremer, Opera Bot. 40: 48, 1976.

O. sedifolia (DC.) Anderb. & Bremer, comb. nov. Basionym: *Eclopes sedifolia* DC., Prodr. 6: 288, 1838 (= *Relhania sedifolia* (DC.) Harv.).

O. silicicola (Bremer) Anderb. & Bremer, comb. nov. Basionym: *Relhania silicicola* Bremer, Opera Bot. 40: 56, 1976.

O. squarrosa (L.) Anderb. & Bremer, comb. nov. Basionym: *Santolina squarrosa* L., Cent. 2. Plant. 30, 1756 (= *Relhania squarrosa* (L.) L'Hér.).

O. steyniae (L. Bolus) Anderb. & Bremer, comb. nov. Basionym: *Relhania steyniae* L. Bolus, Ann. Bolus Herb. 1: 191, 1915.

O. uniflora (L. f.) Anderb. & Bremer, comb. nov. Basionym: *Athanasia uniflora* L. f., Suppl. Pl. 362, 1781 (= *Relhania uniflora* (L. f.) Druce).

O. viscosa (L.Hér.) Anderb. & Bremer, comb. nov. Basionym: *Relhania viscosa* L'Hér., Sert. Angl. 1: 23, 1789.

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POPULATION STRUCTURE OF THE RECENTLY REDISCOVERED HAWAIIAN SHRUB *TETRAMOLOPIUM ARENARIUM* (ASTERACEAE)[1]

Richard D. Laven,[2] *Robert B. Shaw,*[3] *Patricia P. Douglas,*[3] *and Victor E. Diersing*[4]

ABSTRACT

A demographic monitoring study was initiated in the sole known population of *Tetramolopium arenarium*, a taxon that was considered extinct until recently rediscovered on the Pohakuloa Training Area, Island of Hawaii, Hawaii. Spatial distribution, size structures, life history stage structure and reproductive output were determined for the population. This sole population is restricted to a 100 m by 300 m area along a mesic ridge system and is comprised of 134 individuals. Size class frequency distributions are bell-shaped with the population dominated by large individuals. In spite of large flower and seed production, interpretation of these distributions reveals that this species is either on the verge of extinction or that episodic establishment is necessary to ensure the long-term persistence of this rare taxon. In order to safeguard this species, we recommend that military operations and hunting activity be restricted and that the area be fenced to exclude feral animals.

As part of the U.S. Army's Land Condition-Trend Analysis Program, a comprehensive vegetation inventory was conducted of the Pohakuloa Training Area (PTA) on the Island of Hawaii, Hawaii (Fig. 1). During the inventory, *Tetramolopium arenarium*[5] (A. Gray) Hillebr. was collected (Douglas et al., 1989). This taxon was considered extinct because no collections had been made since the late 1800s (Ayensu & DeFilipps, 1978; Lowrey, 1986).

In order to minimize the risk of extinction of this rare species, specific management strategies must be developed for the U.S. Army. A first step in this process is to assess the viability of this population. Because basic population biology may be of more immediate importance than population genetics in determining minimum viable sizes of wild populations (Lande, 1988), we initiated a demographic monitoring study to determine if the population is expanding, stable, or declining. Our specific objectives were: (i) to determine the geographic (site-specific) distribution of the population; (ii) to describe the population size structure and life history stage structure; and (iii) to assess the flowering and reproductive output of the population.

NATURAL HISTORY AND MORPHOLOGY

BRANCHING PATTERN AND PLANT ARCHITECTURE

Tetramolopium arenarium is an upright shrub less than 2 m tall. It has three-dimensional, axillary branching, i.e., sympodial branching related to the development of a terminal, compound capitulescense (Lowrey, 1986). Continuation of longitudinal shoot growth from usually two or three axillary

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[5] The name of this taxon is currently *Tetramolopium arenarium* (A. Gray) Hillebr. subsp. *arenarium* var. *arenarium*. However, because of a typification problem, the plants referred to as subsp. *laxum* from East Maui must be called subsp. *arenarium*, leaving this subspecies from the Island of Hawaii without a name. Therefore, we will not use intraspecific designations and will refer to the plant discussed in this paper as simply *Tetramolopium arenarium*.

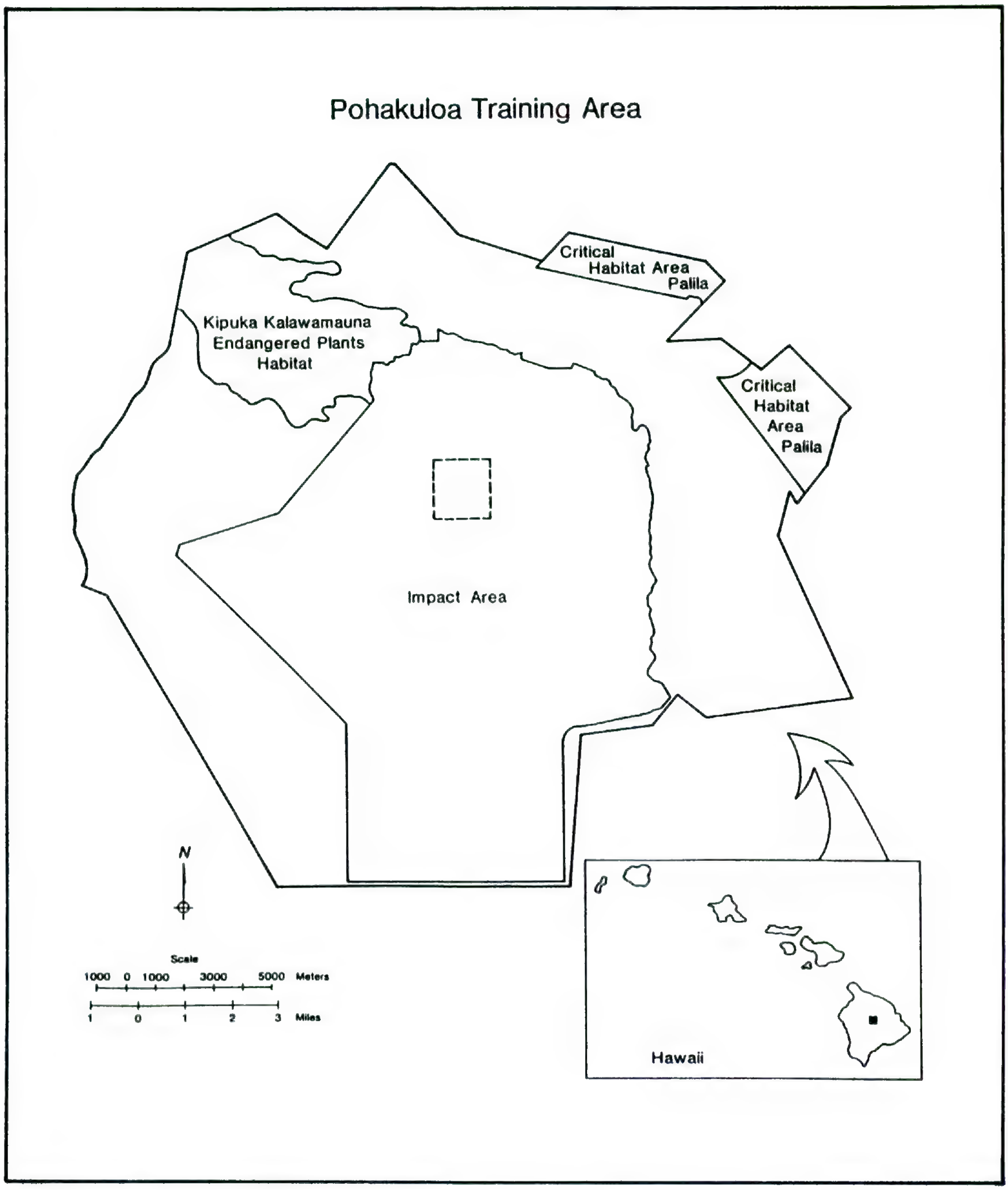

FIGURE 1. Map of Pohakuloa Training Area, Island of Hawaii, Hawaii, showing the location of the Kipuka Kalawamauna Endangered Plants Habitat.

buds leads to development of a terminal capitulescense. Capitulescense development leads to sympodial branching, which occurs repeatedly on the plant (Lowrey, 1986). This distinctive branching pattern is represented in Figure 2 and is consistent with Leeuwenberg's architectural model of tropical trees (Hallé et al., 1978). Because branching phenology is not known, we included the number of tiers for each plant (i.e., the number of sympodial branch nodes) in a model of plant architecture. Our observations indicate that the epicotyledonary tier is the largest, and each successive tier decreases in both length and diameter. We also observed that plants growing in relatively open site conditions were more erect, retained more live and dead foliage, and had longer internodes than plants

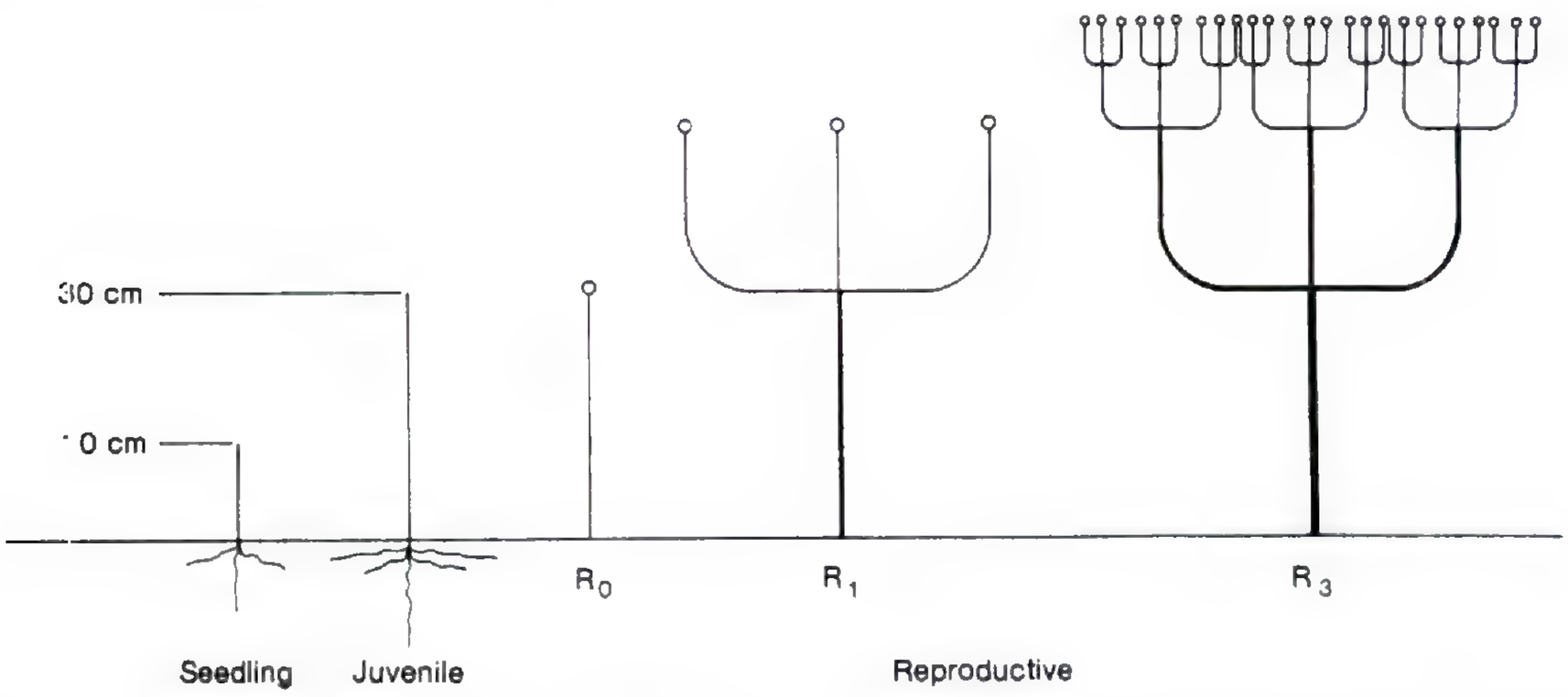

FIGURE 2. Graphical representation of sympodial branching pattern for *Tetramolopium arenarium*, indicating tier and flowering architecture.

growing in relatively dense site conditions. Open-grown plants developed a free-standing, upright "chandelier" morphology. Plants growing in crowded situations were sprawling, and commonly their crowns were interlaced with crowns of other species. We are trying to determine the relationship between the number of tiers, terminal shoots, or capitulescences, and age.

POPULATION BEHAVIOR

Mortality, growth, and reproduction data can be used in a transition matrix to project population behavior over time (Lefkovitch, 1965). This matrix technique can project population dynamics based on size structures or life history stages alone and, consequently, can be used with populations that cannot be aged (e.g., the lack of annuli) or where destructive sampling is not desirable (e.g., extremely small population size).

The projection starts with the size/stage structure at one time and follows the change in structure over one time step as individuals either remain at the initial stage, grow to another stage, or die. Size/stage-specific survivorship, fecundity, and transfer rates project the future of the population (Menges, 1986).

For this species, we have divided the life history into four stages: seedlings, juveniles, vegetative and reproductive (after Menges et al., 1985). Seedlings were arbitrarily defined as those individuals less than 10 cm in height; juveniles were defined as individuals taller than 10 cm and incapable of flowering (i.e., unbranched); vegetative plants have reached the minimum flowering size (i.e., at least one tier) but are nonreproductive (i.e., currently not flowering, but have flowered in the past); and reproductive plants (i.e., currently flowering).

This paper describes the initial population structure. Population projections will be made after changes in the structure are determined, and life history stages may be redefined using Vandemeer's (1978) optimization criterion.

STUDY AREA

The *Tetramolopium* population was rediscovered in the Kipuka Kalawamauna Endangered Plants Habitat (KKEPH) on the northwestern side of PTA (Fig. 1). KKEPH was designated cooperatively by the U.S. Army, the U.S. Fish and Wildlife Service, and the Division of Forestry and Wildlife, Department of Land and Natural Resources, State of Hawaii. Two other endangered plants have previously been located within the Kipuka (Herbst & Fay, 1979): *Haplostachys haplostachya* (A. Gray) St. John and *Stenogyne angustifolia* A. Gray. These two species were once more widely distributed; the extirpation of historic populations apparently has been due to effects of human disturbance, feral animals, and introduced species, rather than volcanic activity (Herbst & Fay, 1979).

Kipuka Kalawamauna is a vegetated, older lava flow surrounded by younger, sparsely vegetated lava flows (Fig. 3). The elevation of the Kipuka is approximately 1,545 m, and it receives about 380 mm of precipitation annually (Douglas et al., 1989).

The *Tetramolopium* population is situated on a mesic ridge system that runs west-northwest (Douglas et al., 1989) with a rockland (rRO) soil type (USDA, 1973). *Tetramolopium* is part of a shrubland community dominated by *Dodonaea viscosa* Jacq. and *Dubautia linearis* (Gaud.) D. Keck.

METHODS

An initial field reconnaissance was conducted to determine the spatial extent of the population. Spe-

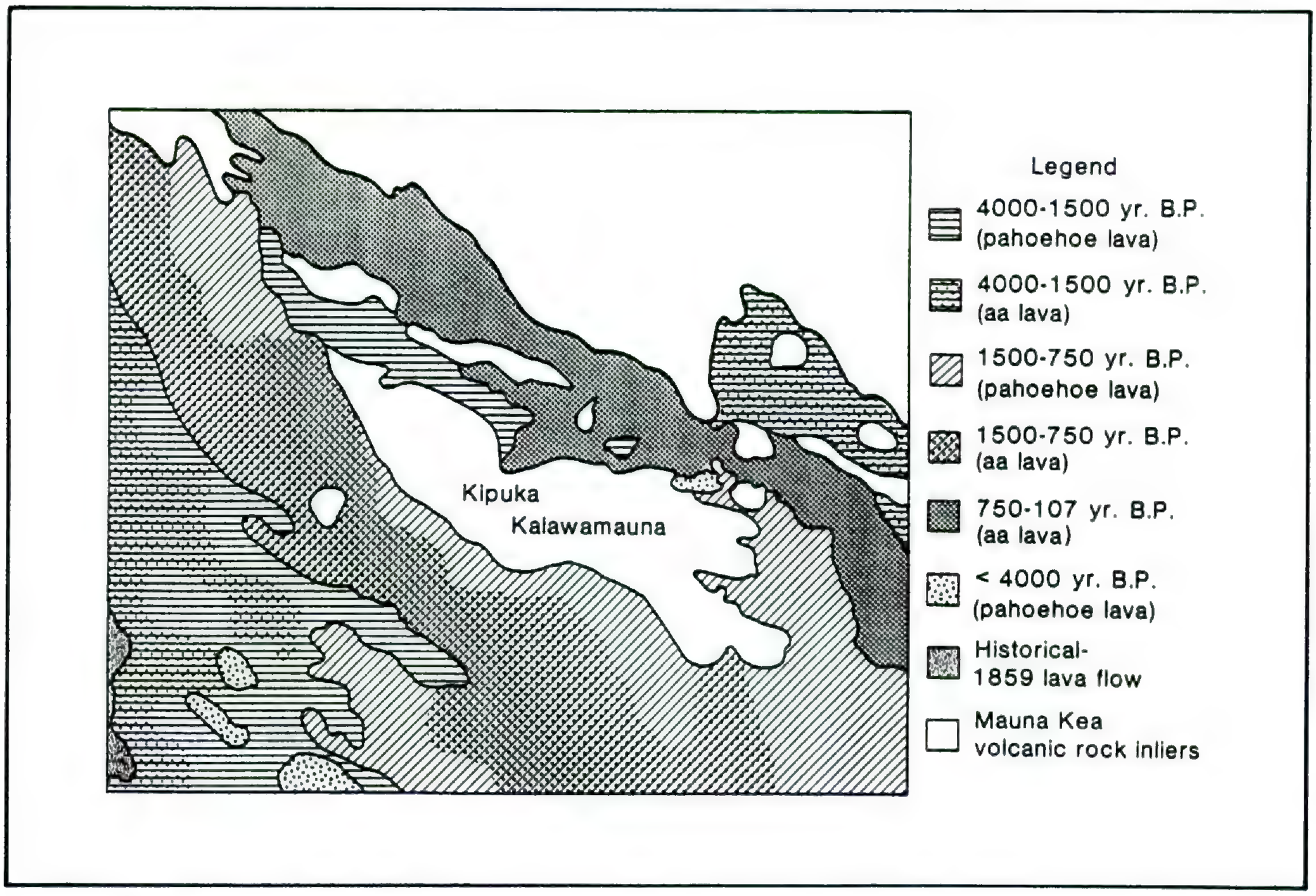

FIGURE 3. Ages of lava flows adjacent to the Kipuka Kalawamauna Endangered Plants Habitat (from Lockwood et al., 1988).

cial care and attention were taken to locate and identify all individuals so that few, if any, were overlooked. All individuals (both alive and dead) were located, affixed with numbered aluminum tags, and mapped. A center line, with known azimuth, was established along the long axis of the population, and individuals were mapped in coordinate space by measuring the distance along the center line and the offset distance (i.e., either left or right of, and perpendicular to, the center line). The beginning and ending points of the center line were permanently marked.

During July and August of 1989, the following data were collected for each individual: total height, basal caliper, life history stage, number of branching tiers, number of capitulescences, and the number of flowering heads per capitulescence. Destructive sampling, in order to assess the possibility of a relationship between size and age, was not conducted because of the small population size.

RESULTS AND DISCUSSION

The sample population is comprised of 134 live and 25 dead plants. As far as we know, this is the sole population of this species; our data are therefore species data and not sample population data. Figure 4 illustrates the spatial distribution of the population. Table 1 presents population percentages by life history stage along with averages for height, basal caliper, tier number, capitulescence number, number of heads, and number of heads per capitulescence.

Mean heights varied by life history stage and ranged from 0.38 m for juveniles to 1.00 m for reproductive individuals. Similarly, mean basal caliper ranged from 3.36 mm to 12.83 mm. Mean tier number also ranged from one for vegetative individuals to nine for the reproductive stage. The reproductive individuals averaged 35 capitulescences and 308 heads (capitula) per plant, leading to a mean of 9 heads per capitulescence. Figures 5, 6, and 7 illustrate the height class structure, basal caliper class structure, and tier number structure, respectively, by life history stage for the entire population.

Age class structures or distributions commonly have been used to interpret and predict population dynamics. Also, age distributions often have been inferred from plant size where age determination was either infeasible or impossible. In many cases it was assumed that size is correlated with age (Lorimer, 1985). However, if possible, this as-

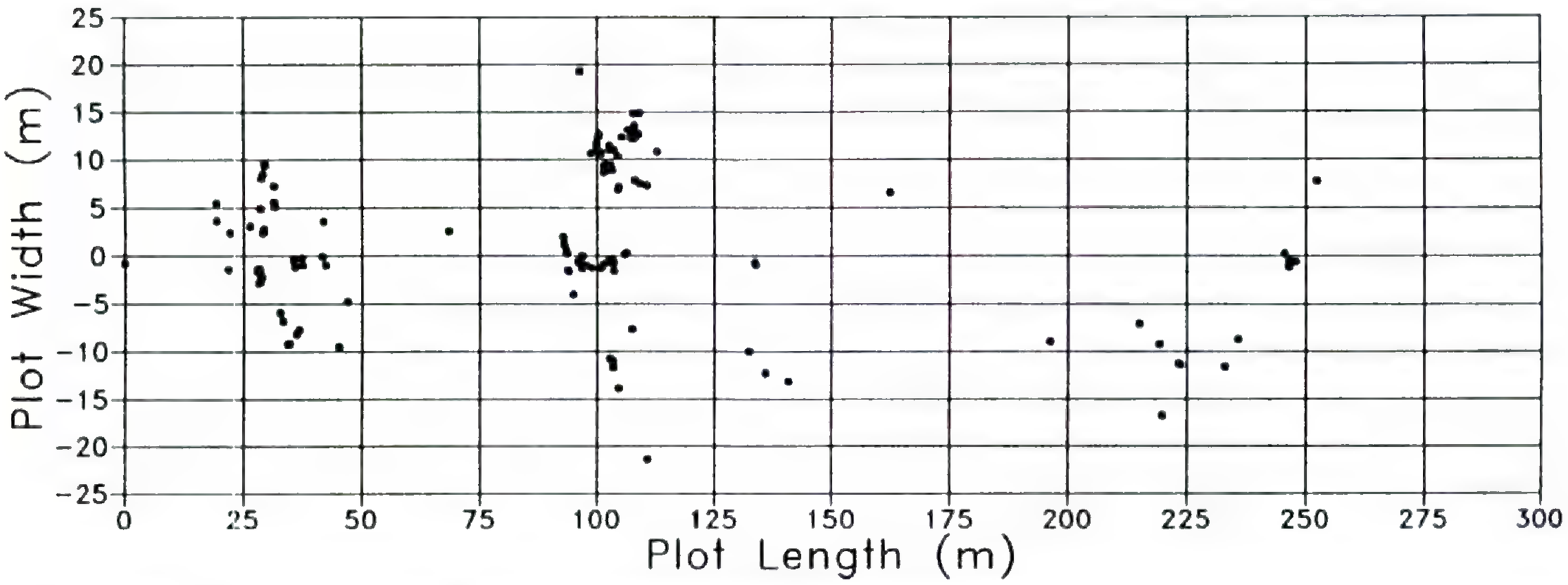

FIGURE 4. Coordinate map of *Tetramolopium arenarium* population illustrating spatial distribution of all individuals.

sumption must be satisfied as prerequisite to the use of size as a surrogate for age. In our study it was not possible to determine plant age because this would entail destructive sampling of an extremely small population without guarantee that a ring structure either exists or is related to age. Until aspects of plant architecture can be related to age, we are compelled to use height, basal caliper, and tier structures in lieu of age structure to interpret population dynamics.

Unimodal (bell-shaped or normal distribution) and descending monotonic (reverse J-shape) curves represent two contrasting size frequency distributions. Unimodal size distributions may represent even-aged populations or multi-aged populations with relatively few seedlings or young individuals (Lorimer, 1985). This type of size distribution has been interpreted to represent a senescent population that is not reproducing and is part of a seral community (Barbour et al., 1987). Reverse J-shaped size distributions typify all-age stands with relatively large numbers of seedlings of young individuals. Barbour et al. (1987) interpreted this structure to indicate a high probability of a population maintaining itself in a relatively steady state community.

Figures 5, 6, and 7 clearly represent the bell-shaped size frequency distribution. These size structures may indicate that the *Tetramolopium* population is in jeopardy with a high probability of imminent extinction. There is, however, the possibility that episodic establishment occurs when environmental conditions are appropriate. Periodic establishment would be sufficient to maintain a

TABLE 1. Population characteristics of *Tetramolopium arenarium*.

Life history characteristics	Number	Average ± Standard deviation		
		Height (m)	Basal caliper (mm)	Number of tiers
Live plants				
Juvenile	7	0.34 ± 0.11	3.16 ± 1.06	0
Vegetative	17	0.59 ± 0.10	5.51 ± 1.59	1 ± 0.70
Reproductive	110	1.00 ± 0.25	12.83 ± 4.65	9 ± 4.65
Total live	134	0.91 ± 0.30	11.39 ± 5.27	7 ± 5.14
Dead plants	25	0.97 ± 0.36	11.08 ± 4.80	7 ± 3.91
Total for all plants	159	0.92 ± 0.31	11.35 ± 5.20	7 ± 4.97

Floristic characteristics	Average ± Standard deviation
Capitulescences	34.81 ± 43.52
Heads	307.63 ± 366.77
Heads per capitulescence	8.95 ± 1.71

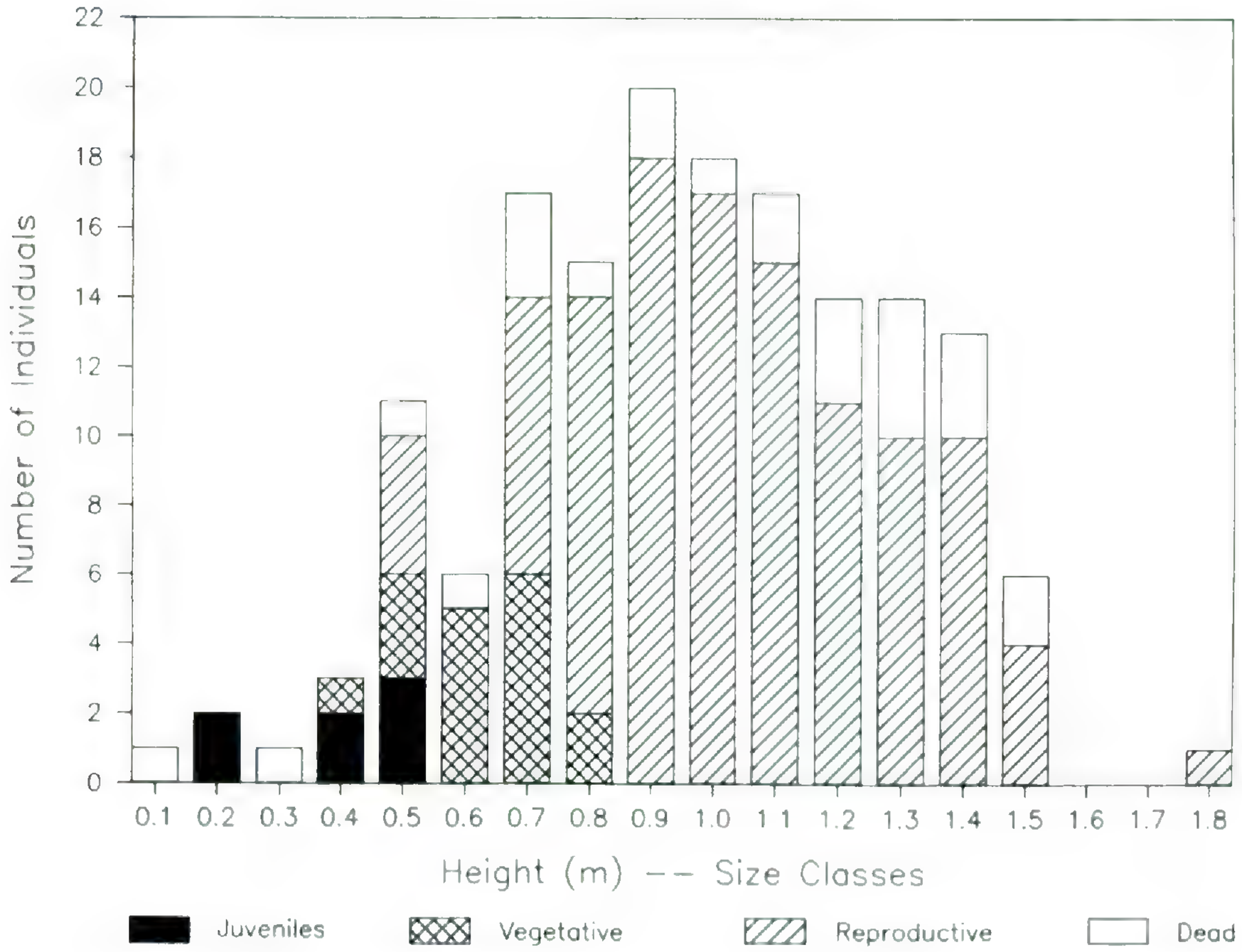

FIGURE 5. Size structure illustrating the number of individuals of *Tetramolopium arenarium* by life history stage for each height class.

population if the individuals are long-lived. Although life span for this species is not known, Lowrey (1986) considered individuals of the genus as probably not long-lived. The paradox, then, is how can a supposedly short-lived population such as this persist in spite of low numbers of small (presumably young) individuals.

In discussing the strategy of Leeuwenberg's architectural model, Hallé et al. (1978) suggested that species with this architecture may tend toward

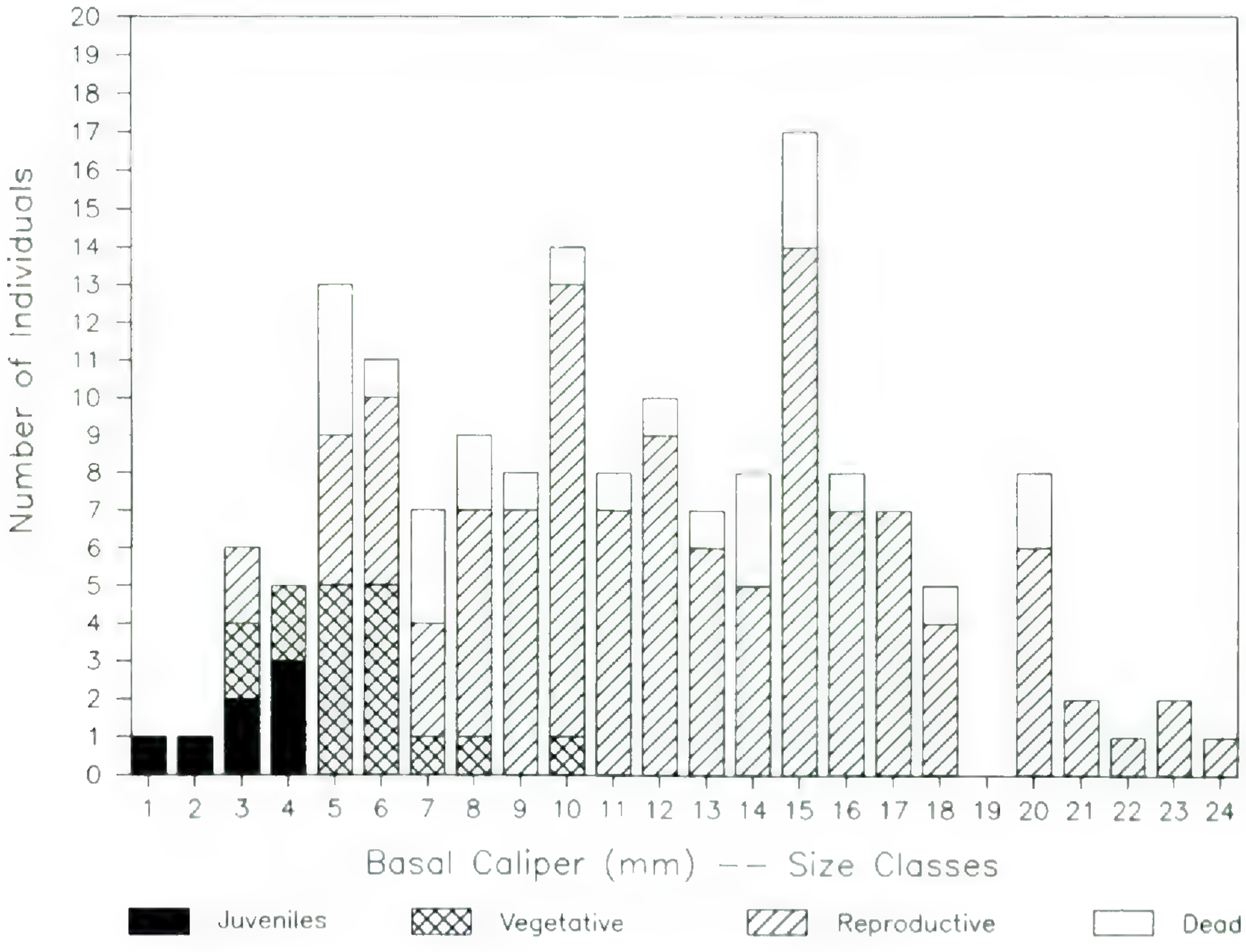

FIGURE 6. Size structure illustrating the number of individuals of *Tetramolopium arenarium* by life history stage for each basal caliper class.

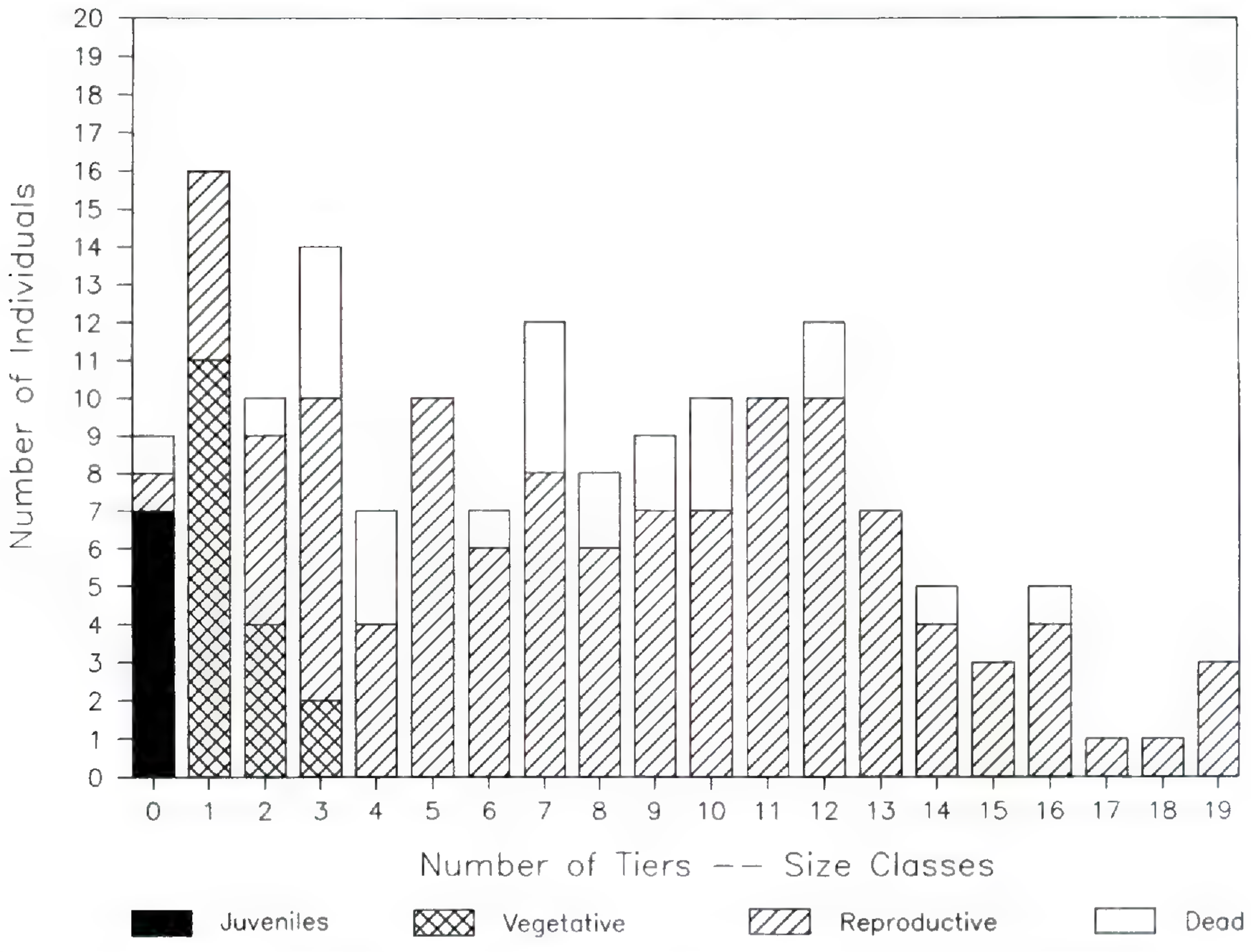

FIGURE 7. Size structure illustrating the number of individuals of *Tetramolopium arenarium* by life history stage for each tier class.

an "r strategy" with rapid establishment rather than individual specialization and long life span. Given the number of heads per plant (Table 1), coupled with Lowrey's (1986) estimates of floret numbers for this species (i.e., 22–45 ray florets and 4–9 disk florets per head), potential seed production may average approximately 10,000 per reproductive plant at any point in time. In light of the observation that flowering occurs in January, April, and August (and likely year-round), *Tetramolopium* appears to have sufficient reproductive output to qualify as an "r-strategist." However, data on seed numbers, germination percentage, and percentage viability, which are necessary to substantiate this claim, are yet to be obtained.

Hallé et al. (1978) also suggested that species with this architecture may be associated with disturbed sites. Although fire history data do not exist, the study site apparently burned within the last decade. *Tetramolopium* has no obvious fire enduring or evading traits and is likely killed by fire, but perhaps fire produces a suitable, ephemeral regeneration environment that facilitates periodic establishment. If this is true, with the proper fire frequency, the size class distributions in Figures 5–7 may result from individuals establishing in the post-fire environment and acting as a relatively even-aged cohort over time. Consequently, periodic establishment may be both sufficient and necessary to ensure the long-term persistence of this extremely rare taxon.

Caution should be exercised when interpreting these figures because of the relatively subjective way in which size classes were chosen. Because we do not know how well size is correlated with age, the possibility exists that individuals assigned to seedling or juvenile classes are simply old plants which, for unknown reasons, have not developed into reproducing individuals. If, with the passage of time, these individuals do not reproduce, our concerns about extinction would be strengthened. Alternatively, by assigning all individuals capable of flowering into either the vegetative or reproductive class (i.e., combining all age classes of branched individuals into only two life history stages), we may be mistakenly overstating our concerns about population decline. This overstatement may be true if individuals mature at different rates due to genetic or microenvironmental factors and continue to reproduce for long periods of time.

However, regardless of which age surrogate is used, the population appears to be declining. This is true even if one of the measures (Figs. 5–7) happens to represent the true age of the population more accurately.

Even if the size class structures suggested a vital, reproducing population, the uniqueness, isolation, and size of this population lead to the inescapable

conclusion that the species is in danger of extinction. Consequently, specific management plans must be developed to maximize the potential for population perpetuation.

Management Implications and Research Needs

Franklin (1980) suggested an effective population size of 500 as a minimum for maintaining long-term viability from a genetic viewpoint. Although this figure is an approximation, Lande (1988), and likely the biological conservation community at large, does not feel justified in blanket application to species conservation. Regardless of the minimum number chosen, *Tetramolopium* is clearly in imminent danger of extinction. Several factors exacerbate the apparent tenuous existence of this species. Military operations, feral animals, exotic plants, and possibly fire should all be considered when management plans are developed for the conservation of this species.

Because of the immediacy of the threat to this species, we suggest the following changes be implemented to ensure its survival:

(1) Military operations should be restricted, including reductions in foot and vehicular traffic to eliminate trampling, dust, and the potential use of *Tetramolopium* as camouflage. Accidental fire from ordnance also should be minimized.

(2) The population should be fenced to exclude feral animals. The activities of feral hogs, sheep, and goats may have direct, deleterious impacts on this species. Additionally, rooting by feral hogs exposes bare mineral soil, a suitable establishment substrate for exotic plants.

(3) This area is currently open to public hunting, and until the effects of hunting activity (including accidental fire) can be determined, the area should be designated off-limits.

Because so little is known about the biology and ecology of *Tetramolopium*, several research imperatives exist. We are initiating studies on reproduction biology (including pollination ecology, germination and seedling establishment requirements, growth rates and longevity), population genetics, and the role of disturbance, particularly fire, in population biology. Development of methods of propagation also will be crucial to ensure the perpetuation of this species. We envision this study and the research imperatives described above as the first steps in a long-term monitoring program. The eventual creation of a suitable database will increase the likelihood of safeguarding this imperiled species.

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NOTES

A NEW SPECIES OF *COSTUS* (COSTOIDEAE, ZINGIBERACEAE) FROM VERACRUZ, MEXICO

Costus L. is a genus of about 90 species, with a pantropical distribution mostly in the Neotropics. The most recent taxonomic studies dealing with the genus are those by Maas (1972, 1977) and Maas & Maas (1990).

Mexico represents the northernmost distribution limit of this genus in America. This genus is represented in Mexico only by five species of subg. *Costus*: *C. comosus* (Jacquin) Roscoe var. *bakeri* (Schumann) Maas, *C. scaber* Ruíz & Pavón, and *C. pulverulentus* C. B. Presl within sect. *Ornithophilus*; and *C. pictus* D. Don, *C. guanaiensis* var. *tarmicus* (Loesener) Maas, and *C. guanaiensis* var. *macrostrobilus* (Schumann) Maas belonging to sect. *Costus*.

Studies carried out during a comprehensive floristic project of the Flora de la Estación de Biología Los Tuxtlas, Veracruz, Mexico (Ibarra & Sinaca, 1987), have brought to light a distinctive new species.

Costus dirzoi García-Mendoza & Ibarra-Manríquez, sp. nov. TYPE: Mexico. Veracruz: Municipio San Andrés Tuxtla, Estación de Biología Tropical Los Tuxtlas, 18°34′–18°36′N, 95°04′–95°09′W, 200 m, 7 June 1989 (fl), *Ibarra 3400* (holotype, MEXU; isotypes, BM, ENCB, K, LE, MO, U, US, XAL). Figure 1.

A *C. picto* D. Don inflorescentia terminali in caule aphyllo (raro 1–2 foliis), callo conspicuo, bracteola puberula, ovario villoso et foliis supra glabris, infra dense velutinis differt.

Plants 1–1.5(–2) m tall, pale green when dry, sheaths, ligules, and petioles sparsely puberulous. Sheaths (4–)4.5–7(–8) × 1–1.4(–2) cm, green; ligule (3–)4–9(–12) mm long, obliquely truncate, mostly dilacerating into fibers; petiole 3–10(–15) mm long. Leaves narrowly to broadly elliptic, (15–)20–27(–32) × 8–15 cm, (1.5–)2.1–2.5(–2.8) times longer than wide, cuneate at the base, with a (1.5–)2–3 cm acumen at the tip, upper surface glabrous, lower surface densely velutinous. Inflorescence ovoid to fusiform, 3–6(–10) × (2.5–)3–4 cm, elongating to 16 × 5.5 cm in fruit, borne on a leafless shoot 20–40(–70) cm tall, or occasionally terminal on a leafy stem. Sheaths obliquely truncate, 4–5(–8) × 1.3–2 cm, minutely puberulous, sericeous at the insertion, reddish to green. Bracts broadly ovate, 2.5–4 × 2–3 cm, acute, coriaceous, exposed part green, glabrous, covered part reddish, puberulous; callus 5–6(–8) mm long, yellowish, rarely inconspicuous; bracteole 1.5–1.8(–2) cm long, sparsely puberulous; calyx 5–9 mm, sparsely puberulous, lobes deltate, (2–)3–4 mm long. Corolla 4.5–6 cm long, bright yellow, lobes narrowly obovate, 4–5 × 1–1.8 cm, the dorsal one to 6 cm long, outer side minutely puberulous, tube 1–2 cm long. Labellum broadly obovate when spread out, 5–6.5 × 3–3.5 cm, yellow, margins crenulate, lateral lobes with a pubescent line inside, with dark red stripes, the middle lobe reflexed, irregularly 3–5 lobulate, tube 2–2.5 cm; stamen narrowly elliptic, 3.3–4.5 × 1–1.2 cm, yellowish white, apex dark red, rectangular, reflexed, anther 8–9(–10) mm, dorsifixed; ovary 4–6(–7) mm, densely villose; style filiform; stigma bilamellate with a 2-lobed appendage and one lunular, ciliate structure. Capsule broadly obovoid, 8–11 × 6–8 mm, densely villose, seeds 4–4.5 × 2.5–3 mm, black, 5–20 per fruit. Seedlings epigeous.

Common names. Bordón, caña agria, caña de venado.

Uses. The local people chew and suck on the stems to satisfy thirst.

Distribution and habitat. *Costus dirzoi* is known only from the Los Tuxtlas region, Veracruz, Mexico, where it grows in primary tropical rainforest but is more abundant in gaps produced by tree falls or edges of the forest and river banks, at elevations of 160–300(–700) m. The aerial parts of the plants show growth quickly after their stems are cut. The fruits and seeds are eaten and depredated (perhaps dispersed) by mice. Flowering occurs from May to June, rarely in August, and mature fruits are found from November to Decem-

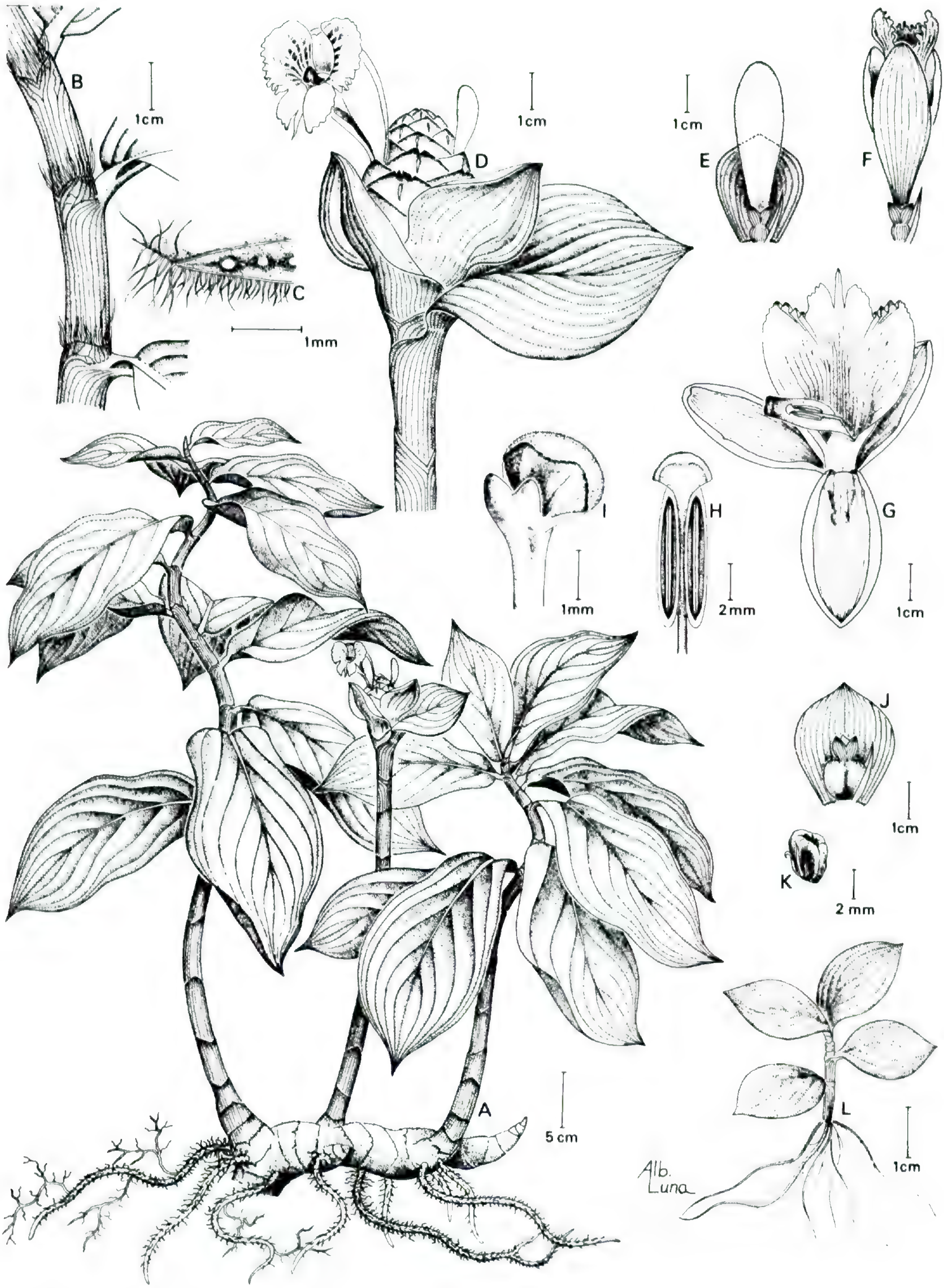

FIGURE 1. *Costus dirzoi*. A–I from *Ibarra 3400*, J, K from *Ibarra & Sinaca 2209*, and L from *Ibarra 1376*.—A. Habit.—B. Part of a leafy stem.—C. Detail of leaf indument, cross section.—D. Inflorescence.—E. Bract and flower bud.—F. Flower.—G. Flower, showing three petals, labellum, and stamen.—H. Stamen and stigma without petaloid part.—I. Stigma seen from ventral surface.—J. Capsule, bracteole, and bract.—K. Seed.—L. Seedling.

TABLE 1. Comparison of morphological features in *Costus dirzoi* and *C. pictus*.

	C. dirzoi	*C. pictus*
Height	1–1.5(–2) m	1–4 m
Sheath and ligule	Puberulous	Glabrous or rarely strigose
Petiole	Puberulous	Glabrous
Lower surface of leaves	Velutinous	Glabrous to densely puberulous, rarely strigose
Length/width ratio of leaves	(1.5–)2.1–2.5 (–2.8)	(2.1–)3.7–4.6 (–5.3)
Inflorescence shoot	Leafless or rarely leafy	Leafy
Callus of bracts	Conspicuous	Inconspicuous
Bracteole	Puberulous	Glabrous to puberulous
Anther	8–9(–10) mm	7–8 mm
Ovary	Villose	Glabrous

ber. The seeds germinate in 2–4 weeks, and seedlings are particularly abundant in February and March. Cultivated plants are found in the greenhouses of Jardín Botánico Francisco Javier Clavijero, Xalapa, Veracruz (29 May 1985 (fl), *Iglesias 23* (XAL)), and Jardín Botánico de la Universidad Nacional Autónoma de México, Distrito Federal.

Additional specimens examined. MEXICO. VERACRUZ: Municipo San Andrés Tuxtla, Estación de Biología Tropical Los Tuxtlas, 31 May 1983 (fl), *Ibarra 641* (MEXU); 9 Nov. 1983 (fr), *Ibarra 996* (MEXU); 25 Jan. 1984 (seedling), *Ibarra 1219* (MEXU); 28 Feb. 1984 (seedling), *Ibarra 1376* (MEXU); 3 July 1984 (seedling), *Ibarra 1843, 1871* (MEXU); 28 Dec. 1984 (fr), *Ibarra & Sinaca 2209* (ENCB, MEXU, XAL); 26 May 1985 (fl), *Ibarra 2439* (ENCB, MEXU, XAL); 15 May 1989 (fl), *Ibarra 3353* (ENCB, K, MEXU, MO, XAL); 22 May 1989 (fl), *Ibarra 3395* (BM, ENCB, K, LE, MEXU, MO, U, US, XAL); 14 Dec. 1969 (fr), *Lot 699* (MEXU, XAL); 26 May 1970 (fl), *Martínez-Calderón 3015* (BM, ENCB, K, MEXU, MO, U, US, XAL); 18 July 1970 (fl), *Martínez-Calderón 3103* (MEXU); 6 June 1989 (fl), *Sinaca 1515* (BM, ENCB, K, MEXU, MO, U, US, XAL); 15 Jan. 1990 (fr), *Sinaca 1564* (ENCB, K, MEXU, MO, XAL); Montepío, some km before Montepío, 2 May 1980 (sterile), *van Rooden 812* (U); Municipio Santiago Tuxtla, 6.5 km de Santiago Tuxtla y 3.6 km camino a Cerro El Vigía, 12 Aug. 1960 (fl), *González & Garza 5599* (MEXU); Municipio de Catemaco, km 18 camino Las Palmas-Catemaco, 6 May 1960, *González & Garza 3333* (MEXU); Municipio de Pajapan, 5 km NW of Pajapan, SE slopes of Cerro San Martin Pajapan, 3 Nov. 1981 (fr), *Nee & Calzada 22759* (XAL).

Costus dirzoi belongs to subg. *Costus* because of its folded bracteole, bilamellate stigma and coriaceous bracts. In addition, the labellum with a short tube and a distinct, exposed yellow limb, with lateral lobes striped with red, permit the placement of the new species in sect. *Costus*. The most closely related species is *C. pictus*, from which it differs by the features shown in Table 1. *Costus pictus* is a plant with a broad distribution range, from southeastern Veracruz to Costa Rica, whereas *C. dirzoi* seems endemic to the Los Tuxtlas region. *Costus scaber* and *C. pulverulentus* are sympatric with *C. dirzoi*, sharing the same habitat. *Costus scaber*, however, differs from the new species in having red-orange bracts and flowers. *Costus pulverulentus*, on the other hand, differs from *C. dirzoi* by its pointed fusiform inflorescence and narrowly obovate leaves.

In order to identify *Costus dirzoi* in the key of Maas & Maas (1990), the eighth couplet needs to be changed as follows and a new couplet, 8A, added. The Maases' use of × to identify second halves of couplets is preserved here.

8. Calyx 5–9 mm long 8A
× Calyx 10–22 mm long 9
8A. Lower side of leaf velutinous; capsule villose; plant green when dry (Mexico) ..... *C. dirzoi*
× Lower side of leaf mostly glabrous; capsule glabrous; plant mostly brownish when dry (Central America and western South America) ..... *C. laevis*

This species is named after Rodolfo Dirzo, who has been working intensively in forest conservation, especially in the Los Tuxtlas area.

We are grateful to Fernando Chiang for the Latin diagnosis and Paul Maas, Patricia Dávila, Fernando Chiang, and María de Lourdes Rico for critical reviews of the manuscript. We also thank Albino Luna for the original illustration and Santiago Sinaca Colin for helping in fieldwork.

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NOTICE

The 1991 Jesse M. Greenman Award

The 1991 Jesse M. Greenman Award has been won by Scott Zona for his publication "A monograph of *Sabal* (Arecaceae: Coryphoideae)," published in Aliso 12: 583–666. 1990. This monographic study is part of a doctoral dissertation from the Claremont Graduate School, Claremont, California, under the direction of Sherwin Carlquist.

The Greenman Award, a certificate and a cash prize of $500, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1991 are now being accepted for the 24th annual award, which will be presented in the summer of 1992. Reprints of such papers should be sent to P. Mick Richardson, Greenman Award Committee, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. In order to be considered for the 1992 award, reprints must be received by 1 June 1992.

Volume 78, Number 2, pp. 273–538, of the Annals of the Missouri Botanical Garden was published on May 1, 1991.

Volume 78, Number 3, pp. 539–855, of the Annals of the Missouri Botanical Garden was published on August 19, 1991.

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The *Annals* publishes original articles in systematic botany and related fields. Text may be in English or Spanish. When in Spanish, an English abstract in addition to a Spanish abstract is required. Papers whose purpose is the establishment of new nomenclature in vascular plants and bryophytes are not accepted. Rather, they should be submitted to *Novon* for consideration. (*Novon* instructions are available from the editor.) Authors are urged to contact the editor prior to submitting manuscripts. Manuscripts sent already reviewed and revised are generally subject to the full normal review process initiated here. Manuscripts not properly prepared may be returned for revision prior to review. This includes manuscripts with improper abbreviations or with diacritical marks not indicated.

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